INTRODUCTION TO
PLANT ECOLOGY

by A. G. TANSLEY

OUR HERITAGE OF WILD NATURE

THE BRITISH ISLANDS AND THEIR VEGETATION

(Cambridge University Press)

PLANT ECOLOGY AND THE SCHOOL (with E. Price Evans)

BRITAIN'S GREEN MANTLE

(George Allen and Unwin Ltd.)

OAKS AND OAKWOODS

(Methuen)

INTRODUCTION TO PLANT ECOLOGY

A Guide for Beginners in the Study of Plant Communities

BY

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PREFACE

THE present work is a thoroughly revised form of my *Practical Plant Ecology*, which was originally published in 1923, new impressions being issued in 1926 and 1932. Not only has the text been brought up to date, but the balance of the book has been to some extent changed. The general exposition of the subject has been added to and strengthened, while those parts of the Appendix to *Practical Plant Ecology* dealing with soil analysis have been omitted, and the sections on Life Forms, on Methods of Vegetation Survey, and on Photography have been incorporated as chapters in the body of the book. In accordance with these changes the title has been altered to *Introduction to Plant Ecology*.

The reasons for these changes are as follows. First of all I have learned that the former book has been widely recommended to students as an introduction to the subject of ecology at large. The demand still continues, though it could not be met during the war owing to the destruction of the publisher's stock and of the plates by enemy action. The type had therefore to be set afresh, and the opportunity arose for a complete revision which should more adequately fulfil the function of a general introduction to the subject.

Secondly, Professor R. C. McLean and Dr. Ivimey Cook, of Cardiff, have published a detailed work on *Practical Field Ecology*,[1] based on long practical experience of field classes of university students, and this will better discharge one of the functions of my original book. Nevertheless I was unwilling to divest the book altogether of its practical character since ecology is pre-eminently a "field subject," and I have accordingly retained most of the matter dealing with field work where I thought it would still be useful to the beginner. But I have

[1] George Allen & Unwin, Ltd.

omitted all detailed instructions for the determination of *p*H, and of the different soil bases, etc. Through the kindness of Dr. W. G. Ogg, Director of the Rothamsted Experimental Station, I have had the benefit of the advice of experienced pedologists—Dr. E. M. Crowther and Dr. R. K. Schofield, of that Station, and Dr. A. B. Stewart of the Macaulay Institute. These authorities, to whom I am much indebted, all agreed that such chemical work on the soil was beset by so many pitfalls as to lead, in the hands of the non-expert, to seriously misleading conclusions and interpretations. What was wanted by the beginning ecologist, they thought, was a general introduction to the soil on modern lines. That I have tried to furnish in Chapter XIV, including, by way of practical work, only such rough field tests and easy laboratory operations as will give the student some idea of the nature of the particular soils with which he is concerned. For exact work the reader is referred to C. S. Piper's *Soil and Plant Analysis* (see p. 238).

On the theoretical side I have included a fuller treatment of the concepts relating to plant communities, re-introducing that of the plant formation in accordance with the definition given in my book *The British Islands and Their Vegetation*. The section on Life Forms, now included as Chapter V of the text, has been re-written and expanded, and the descriptions of the peat communities recast in accordance with modern knowledge. In many other places new passages have been inserted and emendations made. But much of the text remains unaltered.

I am indebted to my old colleague, Dr. W. O. James, of the Department of Botany, Oxford University, for very kindly sending me drawings, reproduced as Figures 15*a* and *b* p .163, of two types of atmometer (evaporimeter) which have substantial advantages over types previously described and which Dr. James has used successfully both in laboratory and field.

The "Classified List of Books and Papers" has been compiled so that would-be students of vegetation may learn what has been done on modern lines in different parts of the country

The bulk of the papers, the great majority of which have appeared in the *Journal of Ecology*, are arranged geographically, and within each subheading in roughly chronological order. The numbers in heavy type attached to the names of authors cited in the text refer to this list.

The fundamental importance of ecology is now increasingly recognised, and the subject is claiming an ever larger part in the development of biological science. Exact quantitative work is beginning to be done over a wider range within its vast field, and to such work, intelligently directed, and to a great increase in our knowledge of all aspects of the life of individual species (*autecology*), progress during the next decades will be mainly due. But the time is scarcely ripe for a detailed handbook of the subject on those lines. The new *Biological Flora*, published in parts (which can be obtained separately) in the *Journal of Ecology* is, however, making an important and substantial contribution to autecology.

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PART I

Introductory

CHAPTER I

What is Ecology?

The word Ecology, as is well known, is derived, like the common word *economy*, from the Greek *οἶκος* (oikos), *house*, *abode*, *dwelling*. In its widest meaning ecology is the study of plants and animals *as they exist in their natural homes*; or better, perhaps, the study of their *household affairs*, which is actually a secondary meaning of the Greek word.

In this book we shall confine ourselves to plant ecology. For various reasons it is more developed and more readily accessible to the beginner than animal ecology. The latter is often not easily attacked without some considerable knowledge of the vegetation, because very many animals depend directly upon plants for shelter, while all depend upon them, directly or indirectly, for food. Plants form the basis of all life as it is lived upon the earth, because they alone have the power of making organic substance from inorganic, of building up living substance from materials like carbon dioxide, water and mineral salts. Animals can only use the results of this work of plants, either by directly eating them (herbivorous animals), or by eating other animals which have fed upon plants. In a favour-

able climate and soil plants cover the ground more or less completely, thus *forming a natural framework or basis for the study of the living populations of the globe.* In this way they determine not only the food but largely also the shelter and general conditions of life of the animal and human communities.

In its widest sense ecology must cover the study of the "household affairs" of animals, including man, not only because animals form an important part of the life existing on the surface of the earth, but because the effects of animals upon plants are numerous and far-reaching; while man of course occupies a unique position owing to his far-extended control over nature. Thus anything like a *complete* study of the ecology of a plant community necessarily includes a study of the animals living in or feeding upon it. The influence of man upon plant communities is of first importance in all but the uninhabited and the most sparsely inhabited regions of the earth. As we shall see in later chapters, we can never afford to lose sight of past and present human activities in their effects on the vegetation of countries which have been long inhabited and densely populated, like those of Western and Central Europe. But though we must thus constantly take account of the effects of animals upon plants, we shall here be concerned entirely with plant ecology—our centre of interest will be the plants themselves.

It is clear that in the wide sense defined above, plant ecology cannot properly be considered a *separate branch* of botany, since it must include a great number of topics which certainly belong to the older, well-recognised divisions of our knowledge of plants. Thus, if we are going to study the household affairs of plants as they grow in nature, we must first of all learn to distinguish the different kinds or species of plants with which we have to deal, and for this purpose we must have some knowledge of *taxonomy*, or, as it is often called, *floristic botany*. To this we must add some knowledge of *genetics*, the modern science of heredity and variation, on

which depend the origin and maintenance of existing "taxonomic units." Then we must understand the *construction* of the plant body, the differences between its different members, how they grow from the seed or from one another—and this is a part of *morphology* or *organography*. Further, we must know something of the *minute anatomy* or *histology* of plants if we desire to penetrate at all deeply into the reactions of plants to the different environments in which they grow. Again, we must study how far plants depend on insects or the wind for fertilisation, or how far they fertilise themselves, the ways in which they spread from place to place, the means by which they propagate themselves and are dispersed (fruits, seeds, rhizomes, runners, etc.). All these last-mentioned topics used to be included under the name "biology," or "bionomics" of plants, but the former name should be restricted to the science of life as a whole, and the latter, which was more frequently used by zoologists, is now generally replaced by the term ecology. Finally, every attempt to ascertain the actual causes that underlie the ability of some kinds of plants to flourish in particular situations, while others cannot, will certainly lead, not only to questions of the means of dispersal already mentioned, and of the influence of animals and of human activity, but also to a study of soil (*pedology*) and climate (*climatology*) in their relation to different species. These last investigations lead directly to a study of the physical and chemical relations of the plant to its habitat, involving some of the most difficult problems of *plant physiology*, problems which occupy the attention of many of the ablest specialists.

Thus it becomes clear that plant ecology in the wide sense is more A MEANS OF APPROACH TO A LARGE PART OF DETAILED BOTANICAL STUDY than a name for a special branch of the subject, such, for instance, as histology (the study of tissues), cytology (the study of cells), or, again, the study of a particular group of plants like the mosses or the fungi. Alternatively, it may be regarded as A SYNTHESIS of the special knowledge obtained by the study of particular departments of botany IN

RELATION TO THE LIFE OF PLANTS IN THEIR NATURAL HABITATS. It is important to emphasise this fact because the modern popularity of ecology depends largely upon it. This popularity represents a reaction from the kind of botany which dealt only with plants in narrowly defined aspects, such as the study of anatomy, of physiology, and of the different groups of the plant kingdom. That sort of study is most conveniently pursued in laboratories to which the plants to be studied are brought, and much of it can only be carried out with the aid of laboratory equipment. The result of the too exclusive pursuit of laboratory work is to remove the student altogether from plants as they actually live in their homes; and in the absence of continual contact with plants in nature his knowledge becomes curiously limited and one-sided, though it may be profound within its limits. Occasional field excursions do not suffice to correct this tendency, for even when taken seriously, (which is not always the case) they are almost always limited to collecting and naming the species met with—there is rarely time for anything more. *Ecology must be studied primarily in the field*, though it is often desirable or necessary to continue in the laboratory the investigation of special points which cannot be decided without books, microscopes, or laboratory apparatus.

A parallel may be found in the study of man. The human anatomist and the human physiologist have, each in his own sphere, a profound knowledge of man, and the two together can give a fairly complete general account of the structure and working of the human body. But no one would contend that such knowledge covers the field of what we may know about man and his activities. It is not sufficient to study the structure of his dead body in the dissecting room, or the functions of his organs and tissues in the physiological laboratory. To learn what man actually is and does in the world, we have to go out into the world and study him as he lives and works among his fellows. And the same is true of plants.

Plants are gregarious beings, because they are mostly fixed in the soil and propagate themselves largely in social masses,

either from broadcast seed (or spores), or vegetatively by means of rhizomes, runners, corms, or bulbs, sometimes by new shoots ("suckers") arising from the roots. In this way they produce *vegetation*, as plant growth in the mass is conveniently called, and this is found to fall naturally into *plant communities*, or *units of vegetation*. Now these plant communities have structures, activities and laws of their own. Each has an internal economy depending on the relations of its individual members to one another; also an origin, history, and fate. Particular communities can exist in some places and not in others, depending on the conditions of soil and climate and on their relations to other plant communities and to animals. Within the larger communities smaller ones exist. In these features we recognise parallels with the nations, tribes, and societies of mankind, though the members of plant communities are not so closely knit as the members of human, and even of the higher animal, communities, by a complex physical and psychical interdependence. Plant communities are also essentially different from human communities, in that they are commonly composed not of a single species of organism, but of several or many different species living together.

The main causes of the specific structure and individuality of a given plant community are: first, the fact that only those species can be present in it which exist in the particular part of the world, and which are able to reach the particular spot; secondly, that only those can be present which are able to exist under the given conditions of life, and in competition with the other species present; and thirdly, that in many communities certain species can only survive in the presence of others, for instance the "shade plants" of a forest floor under the trees which cast the shade.

The systematic study of plant communities is on the whole a modern study, though types of vegetation and their dependence on conditions of life have been recognised for a long time. The active modern study of these types is, however, only about half a century old. In Great Britain especially "ecology"

has tended to become identified with the study of plant communities, because both the general use of the name and the organised study of communities were largely determined by the publication in 1896 of the German edition, entitled *Ecological Plant Geography*[1] of the pioneer work[2] by Professor Warming of Copenhagen. This identification is not, however, justified. As we have seen, ecology in the wide sense is much broader. *Synecology*, from the Greek *σύν*, *together*, is often used for the study of communities, as distinct from *autecology* (Greek *αὐτός*, *self*, *by oneself*, *alone*) for the study of the ecology of individual species. Modern Continental workers, and they are being followed by many American authors, now generally use the term *plant sociology* for the study of plant communities as such. They confine the word *ecology* to the study of the *habitat*, the *oikos* itself, of a plant or of a community, i.e. of the sum total of the effective conditions under which the plant or community lives in a given spot. This is certainly a strictly logical use. Nevertheless, in this book the word is employed in the wider meaning at first described, for it is important, especially in a book intended for beginners, to keep the emphasis on ecology as the approach to botany through the direct study of plants in their natural conditions. In this approach a knowledge of plant communities, their structure, economy, origin and fate (plant sociology) must bulk very large.

Ecology in this wide sense is of the greatest importance in schools, because from the outset it introduces the pupil to plants as they actually exist, and to the parts they play in the world, and avoids the narrow one-sided ways of looking at plants that the older-fashioned methods of teaching botany, if pursued alone, tend to develop.

[1] *Lehrbuch der ökologischen Pflanzengeographie*, Berlin, 1896.

[2] *Plantesamfund: Grundträk auf den ökologiske Plantegeografi*, 1895. "*Plantesamfund*" is roughly equivalent to "Plant Communities."

CHAPTER II

Natural and Semi-Natural Vegetation

By natural vegetation we mean of course vegetation primarily due to "nature" rather than to man. To take extreme cases: A virgin forest is clearly natural, while a wheat or root crop is clearly not. But we have to recognise at once that there are a great many cases intermediate between these two extremes. If we leave out of account all the genuinely virgin, untouched communities on the one side, and all sown field crops and plantations on the other, we find that large parts of the vegetation of a country like Great Britain, more especially of the north and west, but considerable tracts also in the south and east, owe their character partly to nature and partly to human activity. If the vegetation itself is spontaneous, i.e. has occupied the ground without the aid of direct human action, but has nevertheless been partly determined or markedly modified by man or his animals, we class it as "semi-natural."

Thus natural woods which are "selectively" felled (i.e. from which single trees are periodically taken out), but not "clear felled" and replanted, and those which are regularly coppiced; heaths and moors, which are periodically burned or regularly pastured; grassland which has not been sown, but which is regularly pastured or mowed; marshes which are drained and pastured, or periodically cut, are semi-natural vegetation. The great bulk of the forest and "waste land" of the British Isles is in this condition. True "virgin" communities of any size are rare, indeed, practically absent, except on the sea-coast and in the remoter mountain regions. But there are a good many which are substantially natural, having been

interfered with only by occasional felling, pasturing, or burning, and many more which are semi-natural, i.e. which represent a definite modification of a natural community, and are kept in their existing condition only by the activity of man.

The degree to which man has influenced an apparently natural community varies, of course, very considerably, and has often to be made the subject of special investigation. Continued selective felling of the trees in a natural wood, the constant cutting out of certain kinds only, will, for instance, gradually alter the proportional composition of the wood, and sometimes its whole character. Again, the opening of the wood canopy and the consequent letting in of light will kill certain woodland plants and promote the growth of others. It will also allow the entrance of herbs and grasses which could not grow at all in the deep shade, and these will tend to suppress those true shade plants of the woodland floor which have survived, and to compete with the species whose growth has been stimulated, so that the constitution of the ground vegetation may be entirely altered. Pasturing and burning of grassland or heath will destroy some species, and severely check the development of others, while certain species will shoot again quickly after being eaten down or burned, thus altering the composition of the herbage. Others, again, which could not find a footing in the original plant community, will invade burned or very heavily pastured land, because they find there open or sparsely covered spots which would not exist apart from the burning or overgrazing. Lowering the water level of a marsh or fen, or of low-lying alluvial land, by drainage, will kill out certain species and weaken others, while it will admit fresh colonists that flourish in a drier soil. All these effects, and others of a similar nature, have constantly to be taken into account in studying semi-natural vegetation.

A belief is sometimes met with that only perfectly "natural" vegetation is a proper subject for ecological study. If this were true, the ecological field in Great Britain would be very limited indeed. Fortunately, the belief is entirely mistaken. The laws

governing the behaviour of plants, their relations to one another, and their formation of communities, are the same whether the activity of man and his domestic animals plays a part or not. It is true that ecological problems are complicated by man's activity—fresh factors have to be considered. But the plants themselves are working in the same way, tending towards the same effects, whether man is at work or not. The only practical difference is that the plant communities and their distribution (apart altogether from actually cultivated areas) are to a considerable extent changed in countries where most of the land has long been subject to human interference from those still untouched or only slightly touched by human agency.

In the countries which have long been the seats of civilisation it is not always a simple matter to reconstruct the "original" vegetation. But this can usually be done with a fair degree of certainty when sufficient detailed knowledge of the behaviour of the native plants and the communities they form has been obtained and a comparison made with neighbouring countries having a similar climate and flora, but perhaps with different methods of forestry and agriculture. On the other hand, man is always unwittingly performing ecological experiments on a small or a large scale, experiments which the ecologist can watch and the results of which he can trace out and record, thus slowly gaining an extensive knowledge of the capacities of plants, of their reactions to changed conditions, which the observer in a "virgin country" cannot easily acquire.

It is true that the farmer, landowner, or "local authority" sometimes carries his experiments further than the ecologist would desire. The observation of a process of recolonisation of a piece of cleared land, for instance, may be rudely interrupted by digging for gravel, road-making, or building. Interesting and instructive bits of vegetation are often destroyed by some fresh outburst of energy on the part of "higher powers," all the more irritating when it is clearly not wisely directed. But the observer who can put up with such disappointments,

and who will never lose an opportunity of observing and comparing what is going on, can learn a great deal if he will adapt himself to the conditions of the countryside in which he lives.

Even the most highly cultivated parts of the country, where the land is almost all under the plough, offer numerous opportunities for ecological study. Such are great tracts of the eastern counties of England, considerable parts of the southern counties, parts of the Midlands, the south Lancashire and Cheshire plains, etc. First of all there are the roadsides and hedgebanks, which bear semi-natural plant communities—the former, when they are in the form of "grass verges," often very similar to those of pastureland or on barren sands of heathland, the latter consisting mainly of "marginal" woodland species, i.e. those which grow on the edges of woods under similar conditions of soil and climate. These both provide good subjects for study and comparison. Secondly, there are the weeds of the arable land itself, which differ according to climate, soil and crop rotation. And finally there are the crops themselves, which are by no means the least interesting communities, though they are entirely artificial. Scientific agriculture, indeed, is largely applied ecology. The field crops which *can* be successfully cultivated on a given piece of land depend, of course, on the climate and soil, just as does the natural vegetation; but the crops which actually *are* cultivated depend also upon effective demand, upon the existence and accessibility of markets, so far as they are not used locally.

The grass fields of "permanent pasture" which occupy so much of the Midlands and West of England (though considerably less than before the war) are really semi-natural plant communities, for though they may in many cases have been "laid down to grass" by sowing ploughed land with seed, they quickly become modified by the natural immigration of herbs and grasses, so that sometimes few of the kinds of grass sown ultimately remain. The composition of the flora of permanent pasture varies with the soil, the water supply, the proximity of neighbouring natural vegetation, and also with

the kind and amount of pasturing and manuring. The grazing regime is always an important factor.

Plantations of native trees on arable or grassland or on old cleared woodland may develop into communities practically indistinguishable from natural woodland. This is where the same species are used that naturally form woods on the same soil. Woodland plants colonise the plantation, which gradually approximates to the structure and composition of a natural wood—all the quicker, of course, if it was planted on an old woodland site. Woodruffe-Peacock (**167**, 1918) described such an oakwood on clay soil more than a century after it was planted on arable land, and it had acquired the character of a native wood in practically every respect. A large number of spruces had been planted with the oaks, and while some of these were still present, many had gone and none were flourishing: eventually all would surely disappear. Larch failed equally. Ash, wych elm and sycamore[1] were the only trees planted with the oaks that really did well, and these are species that one might find in a natural British oakwood.

Plantations of exotic trees, particularly conifers—spruce, pine and larch are the kinds most commonly planted in this country—provide examples of artificial communities, differing, as regards the ground vegetation, more or less considerably from our natural woods. Sometimes they are invaded by "weeds," sometimes certain woodland plants obtain a footing in the plantation, sometimes the soil remains or becomes practically bare. In any case the plantation affords some opportunity for ecological observation and comparison, even where the results are chiefly negative.

Thus there is plenty of work for the ecologist in highly cultivated districts, though it is not quite of the same kind as in regions which are mainly occupied by natural or semi-natural vegetation. Even building sites and roads which have been laid out and left derelict for a time, and similar places, often present the material for interesting study. Such habitats

[1] Sycamore is not a native tree but has established itself all over the country and behaves just like an indigenous tree.

are not of course natural, either in origin or character. The soil is peculiar—indeed, it is not "soil" in the narrower sense, because it contains little or no *humus* (derived from the decayed remains of plants)—and can only be colonised by a certain selection of species—mostly, though not wholly, the weeds of roadsides or of ploughland. But these species and their powers of colonisation and relative persistence furnish ecological problems of considerable interest. Broadly they behave in much the same way as the first colonists of "natural" dry areas in which there is little or no humus. Where there is much combined nitrogen derived from organic refuse, special kinds of plants will occupy the ground, of which the common stinging nettle is a good example. These *nitrophilous* plants are often specially luxuriant about farmyards, the lairs of cattle, and similar places.

Even when a habitat owes its existence directly to human activity, it may be occupied by a perfectly natural plant community, i.e. a collection of plants whose composition owes nothing to human agency, and might equally well occur in a "natural" habitat. Thus the stones of a wall built of limestone blocks will be colonised by just the same lichens and mosses that cover the surface of natural limestone rocks, the crevices by the same flowering plants and ferns that we find in the fissures of the same rocks. And similarly with a wall of sandstone, or dolerite, or granite. An artificial pond will be invaded by much the same plant communities arranged in much the same way as a natural lakelet on the same soil and in the same surroundings, a canal by the same communities as a sluggish river, and so on.

From all of which we draw the very obvious conclusion that it is not the activity of man at large that is significant to the plant ecologist, it is the actual conditions which he brings about. If human activity destroys a large number of plant communities and plant habitats, and modifies, to a greater or less extent, many more, it also produces fresh habitats and fresh plant communities, and thus provides fresh opportunities for ecological study on every hand.

PART II

Structure, Distribution and Development of Vegetation

CHAPTER III

The Units of Vegetation (Plant Communities)

SINCE plants are, for the most part, gregarious in their occurrence, we can never get any deep insight into their "household affairs" unless we consider them as members of the communities in which they naturally grow. The "ideal" method of study might be to investigate each species separately, till we knew in detail its life history, the methods by which and the rate at which it could spread, its behaviour under different conditions of climate and soil; and only when we had obtained this knowledge proceed to study the species as it existed in communities along with other species.

This ideal method is, however, quite impracticable. To obtain anything approaching such a complete knowledge of the ecology of any one species would mean many years of observation and experiment entirely devoted to that one species, and it is a fact that we have not yet acquired such a complete knowledge of any single species. It is very much

to be desired that those who have the time, opportunity, and taste for such detailed and thorough *autecological* studies should undertake and carry them through. As a result of such work we should be in a very much better position to attack the problems raised by the various plant communities than we are at present. Careful and thorough work of this sort is indeed one of the greatest needs of ecology. Some suggestions as to the lines on which it can best be pursued will be found in a later chapter.

Meanwhile we need not and cannot wait till such work has been done before tackling plant communities themselves. There are many things we can find out about the communities before we possess an exhaustive knowledge of the autecology of the individual species which compose them. Indeed, the study of a community is one of the best ways of suggesting the most important problems presented by the individual species of which it is made up. The study of a plant community always and necessarily drives us back to the individual species, and we begin to realise at an early stage how little we know about them. In this way our interest in purely autecological problems is most likely to be aroused and sustained. No apology therefore is needed for beginning with *synecology*. It goes without saying that it is essential to be able to distinguish and name accurately the species of which the communities to be studied are composed.

PLANT COMMUNITIES ON A COUNTRY WALK.—If we take a walk through the English country-side and attend to the vegetation around us, we shall be able to distinguish without difficulty the purely artificial or culture communities, such as cereal, root, mustard, or clover crops, plantations of larch or spruce, from the natural and semi-natural vegetation of various grades. The exact degree to which these latter have been determined or affected by man may be a matter of more difficulty.

The meadow through which our footpath leads (permanent

pasture or hay crop) is obviously mainly so determined, though the plants may all be genuine natives. Here we have an example of a plant community determined by man but dominated by different species of native grass.

The copse which we presently pass has a different status. It may have been planted, but it may be a modified remnant of primitive woodland. The dominant trees and shrubs are very likely those which would have been there in any case, though their form and perhaps their relative proportions have been determined by felling and coppicing. The copse, then, is quite possibly a modified example of the natural forest community, dominated very probably by oak and hazel.

Presently we come out on to a stretch of heath dominated by the common ling (*Calluna*). This is very likely determined by a difference of soil corresponding with a distinct geological formation, for instance a sand. It may be kept in its condition as heathland by pasturing or burning, or both, and this may be evidenced by the birches, in many places pines, and sometimes oaks, which grow on its edges, and by the patches of scrub or single bushes dotted about it. These may represent the efforts of woody vegetation to reconquer the ground, efforts which would soon be successful if it were not for the constant attacks of grazing animals. On the other hand, the soil may be unsuitable for tree growth, as shown by the yellowing and dying of young oak seedlings. The heath, then, is certainly a natural or semi-natural community, quite distinct from the meadow and the copse. It may be a stage in the development of forest, or it may represent the only type of vegetation the particular soil and climate could naturally produce.

In wet hollows of the heath there will be collections of species different from those of its general surface, for instance the cross-leaved heath, the purple moor grass, and perhaps bogmoss, butterwort and sundew. Here is another distinct community, evidently determined by the wet soil, and also, as we should learn by further comparison, by the very acid soil water.

Beyond the heath area we will suppose the ground slopes down to a riverside, bordered by a belt of fen or marsh, liable to be flooded by the river after heavy rains. The fen or marsh represents yet another plant community, covered with species of grass and sedge, among which may be many other plants which only grow in wet places, but different from the plants of the wet hollows in the heath. The soil of the fen or marsh may contain the same amount of water as that of the wet heath, but it is not acid, and supports quite a different vegetation.

The edge of the river itself may be lined by a reed swamp, composed of tall grasses, sedges, or bulrushes. In the water are other plants, with floating leaves if the stream is sluggish; and others again wholly submerged. All these last-mentioned communities are essentially natural, though they may be modified by human activity in various ways.

It is very easy to see that the various units of vegetation are not all of equal rank. Thus within an oakwood you may have a localised belt of ashes or alders following the banks of a stream, or a patch of bluebells in one place and not in another; on a heath you have local patches of a species of grass or of moss. And clearly you cannot consider the lichens covering the bark of the trees in a wood as a community of equivalent status to the woodland itself. Yet all these are units of vegetation. We apply the term PLANT COMMUNITY to any such unit of whatever size or rank. Thus the deciduous forest of Western and Central Europe is a plant community, and so are the submerged water plants in a pond, or the green coating, often largely or entirely composed of the minute alga *Protococcus*, on a damp wall or tree-trunk. *A plant community is any collection of plants growing together which has as a whole a certain individuality.*

The Plant Formation

The largest and most comprehensive kind of plant community is the *plant formation*. Plant formations correspond in

a general way with those plant communities which are recognised in common language as fundamentally distinct *types of vegetation*.

First of all we have the great *climatic vegetation types* of the world, determined by the well marked types of climate prevailing over wide areas of the earth's surface. Some of the most conspicuous and widespread of these are the evergreen tropical rain forests of the Indo-Malayan region, of parts of equatorial Africa and of central America; the deciduous "summer" forest of western and central Europe, of the eastern states of North America and of parts of eastern Asia; the northern and subalpine forests of needle-leaved coniferous trees; the temperate climatic grasslands (prairies and plains) of the United States and Canada, and the steppes of southern Russia; the deserts of North Africa and south-western Asia, of parts of South Africa, of Chile and of parts of western North America. Each of these regions is characterised by a specific kind of vegetation, "formed," in a very real sense, by the prevailing climate, and known as a *climatic* plant formation. The European deciduous summer forest formation, to which our own native deciduous woodlands belong, has the same general characters as that of eastern North America because it exists in the same general type of climate, and both formations belong to the same *formation-type*. Similarly the tropical rain forest formation of Indo-Malaya has the same general character as that of West Africa and of Central America and belongs to the same formation-type, though each of these formations has its own peculiarities.

Besides the great climatic formation-types there are others determined, not *primarily* by climate, but by conditions such as the general nature of the soil which they occupy. A good example is the *reed-swamp type* which grows in shallow water on the edges of lakes and slow rivers all over the world, vegetating in soft water-logged mud or silt and in some places (e.g. the delta of the Danube) where this kind of soil is very extensive, covering vast tracts of country. Such a formation-type

is largely independent of climate, though the particular reed-swamp formations of different parts of the world differ in the particular species of which they consist. Other formation-types, determined in a similar way and more or less independent of climate, are the sand dune and salt marsh formation-types, which are also primarily determined by the soil and other local conditions in which they grow. All these formations, determined primarily by soil, are called *edaphic formations* (Greek ἔδαφος, *edaphos*, the soil, ground) in contrast with the climatic.

There are, however, some formations, such as the *heath formation*, which are determined partly by soil and partly by climate, i.e. they can only exist within rather a narrow range of climatic variation and in suitable soils. This shows that plant formations cannot always be rigorously divided into climatic and edaphic; but appropriate climatic conditions naturally have to be present.

Formation-types can also be recognised in semi-natural vegetation. Such a formation-type is the pastured grassland of western Europe, which is determined not only by climate and soil but also by the specific and continuous operations of man (*anthropogenic formations*). The human activity involved —burning, pasturing, mowing, etc.—has to be taken as one of the constant factors of the habitat—indeed as the differentiating or *master factor* (see p. 38).

A general feature of all formation-types is that the *dominant plants* of the formations belonging to each are characterised by particular *life forms*. By dominant plants we mean those plants which give the community its characteristic appearance or physiognomy and which may also largely control its structure, for example the trees of a forest, the low-growing undershrubs of a heath, or the typical grasses of a meadow. By life form is meant the type of plant body, with which is associated its life history. Thus the deciduous broad-leaved tree (oak, elm, ash, beech, etc.) is a well-marked life form; the evergreen needle-leaved tree is another; a third is the perennial herb with a persistent underground stem (rootstock) and leafy aerial shoots

which arise from fresh buds every spring and die down in the autumn; a fourth is the annual herb whose whole vegetative body dies every season, the species being continued from year to year by means of seed; and so on. The oldest and most obvious division of the life forms of the higher plants is into trees, shrubs and herbs, but each of these includes several distinct life forms—the herbs a great number. Some account of life forms is given in Chapter V.

The European summer forest formation—the native woodland over much the greater part of the British Isles—is a north-western extension of the continental forest which is dominated by species of deciduous broad-leaved trees—a life form that is adapted to the climatic conditions of western and central Europe. In central and northern Scotland this formation is partly replaced by pine forest, which may be regarded as a south-westward extension of the Scandinavian coniferous forest dominated by evergreen needle-leaved coniferous trees adapted to the northern climate where snow lies for the long period of winter.

In most of the British area formerly occupied by deciduous forest this has been replaced by the semi-natural formation of pastured grassland dominated by the meadow-grass life form —besides of course the arable crops and plantations of alien trees, which are neither natural nor semi-natural. Within the same area, also, there are several edaphic formations, such as those of freshwater plants, reedswamp, and the maritime formations of salt marsh, sand dune and shingle beach, besides others, like the heath formation, which are determined partly by soil and partly by climate. Of these last the bog or "moss" formation is another good example. In the very wet climate of western Scotland and western Ireland, great tracts of flat or gently sloping undrained or poorly drained ground are covered with *blanket bog*, dominated sometimes by bog-moss and sometimes by members of the sedge family. The blanket bog is clearly dependent on the wet climate, but wherever adequate drainage frees the soil from the water-logged condition, quite

different vegetation appears, so that adjacent well-drained slopes are occupied by heath, scrub, or even woodland. The bog or moss formation, dominated by the same or similar plants, also appears in less wet climates under special conditions, i.e. where the soil is water-logged and also acid, as in constantly wet hollows in heath (p. 29) and in the so-called "raised bogs" (see p. 70).

The Plant Association and Consociation

The actual units of natural and semi-natural vegetation we find in the field belonging to one of the plant formations are of various nature and status. The largest of them, which are dominated *by particular* species, are called plant *associations* and *consociations*, the former dominated by more than one species, the latter by single species. Thus an oakwood, dominated by one of the oaks, *Quercus robur* or *Quercus sessiliflora*, or a beechwood, dominated by the common beech (*Fagus silvatica*), is a consociation, while a wood dominated by more than one kind of deciduous tree is an association. Oakwood, beechwood or mixed wood, all belong to the European deciduous summer forest formation characterised by the dominance of the deciduous tree, but each by particular species of tree. Similarly the European reedswamp formation shows consociations dominated respectively by the common reed (*Phragmites communis*), the reedmace or bulrush (*Typha latifolia* and *Typha angustifolia*) and the bulrush[1] or lake reed (*Scirpus lacustris*). All three show the typical "reed" life form. Sometimes they grow intermingled (association), sometimes separately (consociations).

All species found in an association or consociation other than the dominants may be called *subordinate* species. These are strongly influenced and often largely determined by the presence of the dominants, and sometimes because the growth and decay of the dominants produces a special kind of humus or otherwise

[1] The name "bulrush" is sometimes given to *Scirpus lacustris*, sometimes to *Typha*. The former use seems to be more "correct" but the latter is quite common.

affects the nature of the soil. A well-defined association or consociation contains subordinate species (1) strictly confined to it (*exclusive species*), (2) seldom met with outside it, or (3) at least found more often within than outside the particular community (lesser degrees of exclusiveness). Species which are present in every example or nearly every example of an association or consociation, whether they are met with outside it or not, are called *constants*. Both exclusives and constants are known as *characteristic species* of the community. Species which occur as often outside as within the community, and those which are found quite rarely and casually within its limits are known respectively as *indifferent* and *casual* species.

The constants of an association or consociation can be determined by comparing the complete lists of species from a sufficient number of examples, the exclusive species only by comparing the lists with similar lists from other communities. The complete list of species, made by combining the lists from a great number of different examples, gives the *floristic composition* of the association or consociation for the area from which the examples were taken. Thus the association or consociation is characterised first of all by the life form of the dominants, i.e. by the formation-type to which it belongs, and then, floristically, by the dominants, the characteristic species, including constant and exclusive species, and the whole floristic composition.

The technical name of a consociation is formed by the stem of the generic name of the dominant with the suffix *-etum*, followed by the name of the species in the genitive case: thus the beech consociation is *Fagetum Fagi silvaticae*, shortened to *Fagetum silvaticae*. Where there can be no possibility of mistake about the species the consociation may be called simply *Fagetum*. Associations have to be designated by joining their names with hyphens, thus beech-oak or *Fagus-Quercus* association.

Habitat and Ecological Factors[1]

The *habitat* of a plant community is defined ecologically, as *the sum total of the conditions of environment* (*ecological factors*) *which are effective in determining the existence of the community in that place.* Thus the general habitat of one of the great climatic plant formations is coextensive with the area covered by the corresponding climate which stamps the vegetation with the characteristic life form of the formation, closely adapted to the prevalent climatic complex.

The European summer forest formation may be taken as an example. The characteristic life form of summer forest is the deciduous tree, which drops its leaves in autumn and produces a fresh crop in spring. The warm and not too dry summer is favourable to the functioning of the rather delicate leaves of the deciduous summer-forest trees. In winter the soil is often too cold for the active absorption of water by the roots of the tree, and if the foliage persisted through winter the tree would run the risk of being killed by the ill-protected leaves continuously evaporating water which could not be replenished from the soil. The trunk, branches, twigs, and winter buds are covered with a bark and with waterproof bud-scales which prevent any considerable loss of water by evaporation during the winter. Thus within this particular climatic region deciduous summer forest is the natural type of vegetation *in the absence of other factors definitely adverse to the growth of deciduous trees.*

Such factors may be marked local variations of climate within the general climatic region, for example in places exposed to particularly violent winds where forest trees may be reduced to the condition of wind-cut scrub or prevented from establishing themselves altogether. Other adverse factors are of a different kind, and of these the most important is the nature of the soil (*edaphic factors*). The climatic plant formation of deciduous trees in one or other of its associations or consociations, can establish itself on a wide range of soils, but there are

[1] A detailed account of habitat is given in Part IV (Chapters XIII–XV).

some on which it is replaced by other formations adapted to the particular soil conditions. Thus in western Europe deciduous forest often finds difficulty in colonising very shallow soils over rock and also the drier and more sterile sandy soils, where it is replaced by heath. And not only are trees unable to colonise the submerged soils of bodies of water, the characteristic climatic dominants such as beech and oak cannot establish themselves as dominants unless the soil is free from continuous water-logging. In the shallow water on the edges of lakes we have, instead, reedswamp, and, on the soils saturated though not covered with water, marsh, fen or bog vegetation, or special trees or shrubs which can tolerate these conditions, such as alder and willow. Deep water, reedswamp, fen and bog, each has its own characteristic life forms, well adapted to the particular conditions in which it grows and widely different from that of the deciduous forest tree, though all exist in the same general climate.

Besides climatic and edaphic factors there is a third class, *biotic factors*, due to the effects of other organisms, and those arising from human activity (*anthropogenic factors*), which bring about much of the semi-natural vegetation discussed in Chapter II, very largely as the result of the continuous grazing of man's flocks and herds.

Particular types of climate like those determining the great climatic formations are, as a rule, far more widely extended over great continuous areas of the earth's surface than the variations of soil and soil water which determine formations like reedswamp, or the conditions of constant pasturing or burning which determine formations like the English chalk pasture or many of our heaths. Thus within the areas of the great climatic types various edaphic and biotic factors give rise to edaphic and biotic formations dominated by life forms very different from those of the climatic formations. Such local formations are by no means always limited to the area of one climatic formation. Thus the reedswamp formation type, with its tall reedlike stems or leaves, and rhizomes creeping in the

soft mud or sometimes floating on the surface of the water, *occurs in tropical and subtropical* as well as in temperate climates, because the edaphic factor of water-logged soil overrides the climatic factors. Reedswamp is however represented by different associations and consociations, dominated by different species in various parts of the world.

Thus we can recognise, in the case of any formation, determining or *master factors*, whether climatic, edaphic or biotic, which separate one formation from a neighbouring one. For instance a reedswamp on the edge of a river may be adjoined by a strip of pastureland; above this, on a gently sloping hillside, is oak forest. The master factor of the habitat separating the pasture from the wood is biotic, namely the grazing, which prevents the seedlings arising from acorns falling in the pasture from growing into trees. The master factor which differentiates the reedswamp from pasture and forest alike is the high water level (normally above the soil surface) at the edge of the river. The general features of the climate (rainfall, humidity of the air, temperature, etc.) permit the existence of all three formations, but are primarily expressed by the forest which is not exposed to the other (limiting) factors, while the other two are differentiated, the one by biotic, the other by edaphic factors.

The existence of associations and of separate consociations within a formation often depends upon minor differences of habitat. Some parts of the general habitat may be rather more suitable for one dominant and some parts for another, while other areas again are intermediate, showing no great advantage for any one of the dominants, so that mingling of the dominants (*codominance*) occurs. Sometimes one of the dominants completely occupies an area to the exclusion of the others, though the habitat seems equally suitable for all. This may be due simply to the fact that the occupying dominant got there first, and prevented others from coming in. Such relations exist between oak and beech in the summer deciduous forest, and between bulrush, reedmace and common reed in reedswamp. There are many forests in which beech and oak flourish side

by side, though beech is excluded from some habitats (heavy wet soils) which oak can occupy, and oak from some shallow soils which beech can colonise. Bulrush and reedmace tend to occupy deeper water than the common reed, but the three dominants are often mixed.

The subordinate species of an association often occur throughout segregated consociations as well, but there are frequently some species peculiar to each consociation because the local characters of the habitat (e.g. of the soil) which suit the dominant also favour particular subordinate species, or because of the direct effect of the dominant on the subordinate vegetation. Thus the shrubby and herbaceous vegetation of oakwood and beechwood contain most of the same species, but the deeper shade of a beechwood together with the shallow-rooting habit of the tree tends to exclude shrubs from the undergrowth and also reduces the general ground flora characteristic of oakwoods, while the occurrence in beechwoods of other species which are not found or are much less commonly found in oakwoods is associated with the more persistent humus and with the particular soils commonly occupied by beechwoods in this country (shallow chalk soils and sandy soils).

Strata or Layers of Vegetation

The great majority of associations and consociations, all those in fact whose dominants are tall plants, have distinct *strata* or *layers* of vegetation below the dominant stratum. Thus an English wood commonly has four strata:—(1) The tree stratum, (2) the shrub stratum, (3) the field or herb stratum, (4) the ground or moss stratum. Some woods have two field strata—consisting of tall and short herbs respectively, and there is sometimes a second stratum of lower trees beneath the shade of the dominants. Tropical rain forest may have seven or eight distinct strata of vegetation.

Each stratum has an environment or habitat which differs from that of the others. Thus the crowns of the trees of a wood

are exposed to full sunlight, and often to considerable wind, while all the other strata are more or less protected from both. The protection increases as the soil level is approached, so that the shoots of the lower strata are not only increasingly shaded, but are surrounded by a damper atmosphere, and enjoy a more equable temperature. The roots of the different strata also often have very different environments. Thus the tree roots may occupy partly the soil and partly the subsoil or the cracks in the surface layers of underlying rock where this is near the surface; the roots of the herbs may be partly in the soil and partly in the surface humus; while those of certain herbs and the rhizoids of the mosses are confined to the surface humus.

A herbaceous marsh or fen community commonly has at least three strata—the uppermost consisting of the tall dominant grasses or sedges, at least one intermediate stratum of herbs, and a lowermost stratum of mosses and liverworts. The roots of the different strata (or of different species whose shoots are in the same stratum) may occupy different layers of soil, with, for instance, very different air, water and nutrient contents. A grassland community is similarly stratified. In a comparatively damp climate like that of Great Britain the lowermost stratum of many communities consists of mosses.

The different strata of an association are in a certain sense distinct communities. Each has a floristic composition, dominants, and a "structure" of its own; and the species of each often belong to quite distinct life forms. Each stratum, as we have seen, has a habitat which differs, sometimes very widely, from those of the others. Thus the different strata must always be considered separately in ecological study. On the other hand, the structure and often the existence of the lower strata depends upon the existence and nature of the upper ones. The shrubs of a wood will be much less dense if the tree canopy is heavy. The field stratum may scarcely exist if the shrub layer is very dense. Thus the different strata of a plant association are to some extent comparable with "social strata," classes, or castes of a human community, for we find the same differences of

habitat within the common habitat of the whole community, and a similar dependence between one and another. Each requires separate study from the sociologist, but the whole community to which they belong forms the essential primary unit alike in human populations and in vegetation.

The Seasonal Aspects of a Community

In a climate with well-marked yearly seasons different species of a community come to the height of their vegetative growth, flower and fruit, at different periods of the growing season. These activities of different species are scattered throughout the whole season, but the species tend to fall into distinct seasonal groups. In the British deciduous woodland, for instance, there are five such seasonal groups of species, and the flourishing of each gives a distinct seasonal *aspect* to the community. Thus we can distinguish (1) the *prevernal aspect* of early spring (March and the first half or two-thirds of April in southern England[1]), marked by the coming into prominence of such plants as dog's mercury (*Mercurialis perennis*), celandine (*Ficaria verna*), wood anemone (*Anemone nemorosa*), and primrose (*Primula vulgaris*); in (2) the *vernal aspect* (end of April and May), the trees come into leaf and flower, and in the ground vegetation the bluebell (*Scilla non-scripta*), stitchwort (*Stellaria holostea*), weasel snout (*Galeobdolon luteum*), etc., flower; in (3) the *æstival* or *summer aspect* (June–August), a number of other species become prominent; (4) the *autumnal aspect* (September–November) shows very few or no fresh flowering plants in the woodland, but is marked by the appearance of many fungi; (5) the *winter* or *hiemal aspect* (December–February) is marked by the flowering of winter aconite (*Eranthis hiemalis*) and snowdrop (*Galanthus nivalis*):[2] it is of course rela-

[1] These times are of course only approximate, depending as they do, not only upon the latitude, altitude, soil and exposure, but also on the weather of the particular season, especially in the spring.

[2] Neither of these plants is a native, though both may be naturalised in woodland vegetation close to human habitations.

tively a resting period for most of the vegetation, but the underground parts of many plants continue to grow slowly.

We must be careful to distinguish the growth and activity of the leafy shoots of a plant from its flowering, though these are sometimes contemporaneous. The hazel (*Corylus avellana*) flowers in the hiemal and prevernal aspects, but its leaves do not appear till the vernal. Dog's mercury (*Mercurialis perennis*) flowers in the prevernal or early part of the vernal aspect, while its leaves are active in the prevernal and vernal and right through the summer aspect. The meadow saffron (*Colchicum autumnale*), on the other hand, produces its leaves in the prevernal aspect, but its flowers do not appear till the autumnal, long after the leaves have disappeared. Under the different aspects we have therefore to note what plants are in a state of vegetative activity, as well as what plants are in flower.

Deciduous woodland is characterised, in its field stratum, by rich prevernal and vernal vegetation, though it also contains many æstival species; grassland is mainly vernal and æstival, but is active to some extent throughout the year according to the weather; while heath, fen and salt marsh are essentially summer vegetation continuing into the autumn.

The Plant Society

Within an association or a consociation certain species other than the general dominants form communities of lower rank. These *local* communities are called SOCIETIES. Examples are societies of wych elm in an ashwood, of ash or alder in the damper parts of an oakwood, of tor grass (*Brachypodium pinnatum*) on the chalk downs of south-eastern England, of mosses belonging to *Polytrichum* and other genera on heaths, etc.

A society has usually a single dominant, which may occupy the ground to the exclusion of the association dominants. Sometimes the subordinate species within the limits of the society differ markedly in relative frequency from those of other parts

of the association. Thus a society of a tree, such as the sycamore, casting heavy shade in an oakwood, will reduce or cut out many of the species common under the lighter oak-canopy. Sometimes subordinate species occur in a society which are not present or are quite rare in other parts of the association, for instance the moschatel in the societies of dog's mercury in the Derbyshire ashwoods. This may be because the society dominant only occurs in those parts of the association where the habitat is locally different (*habitat societies*), or again because the growth of the society dominant itself creates new local conditions which lead to the great abundance of certain subordinate species, or to the appearance of others not found elsewhere in the association.

The society dominant is a subordinate species when we consider the association or consociation as a whole, but within the society the other species may be subordinate to it. A society, as has been said, is "a dominance within a dominance." When highly organised, it gives a repetition of the structure of a consociation in miniature.[1] The most slightly organised (lowest) form of society is represented by a mere local dominance of a subordinate species of the association (sometimes due to a chance aggregation of seedlings in one place, often to social vegetative growth) without change in the average distribution of the other subordinate species, except in so far as the social species excludes others by mass growth. The most highly organised type of society (approaching the character of a consociation) is represented by a characteristic list of subordinate species differing from that of the association at large (e.g. a society of *Juncus* on the wetter parts of grassland on heavy soils[2]; of *Erica tetralix* on the damper parts of heaths, etc.).

[1] In some cases such societies really represent fragments of a different formation, as with patches of heath on sandy banks in a wood, where the illumination is sufficient.

[2] In this case, as with a patch of heath in a wood, the society dominant has the life form of a different formation, corresponding with the marked local difference of habitat.

STRATUM SOCIETIES.—Societies of a stratified consociation *may involve all the strata, i.e. every stratum may show, within the society, different frequencies of the species of the stratum,* and perhaps some different species from the rest of the consociation. This occurs, for instance, in a wood where the dominant tree of a society has a marked effect on the habitat by casting greater or less shade, or by producing a different kind of humus from the consociation dominant. But other societies may be confined to one or two strata, e.g. the herb stratum, or the herb and moss stratum of a wood; or, again, the shrub stratum alone, e.g. societies of hawthorn. Societies not involving all the strata may be called *stratum societies.* The herb societies of woodland are often numerous and varied, and may or may not be correlated with the habitat conditions. It has been shown in the case of a Cambridgeshire wood (78) that the societies of dog's mercury, of wild strawberry, and of meadow-sweet are closely connected with the summer water content of the soil, and to a less extent with light. In Hertfordshire woods (95), societies of bracken fern and wood anemone, of lesser celandine, dog's mercury, etc., have been shown to depend on soil moisture, humus content, and soil acidity.

"ASPECT SOCIETIES."—Societies confined to one seasonal aspect of an association are sometimes called "aspect societies." But when a given patch of ground is occupied by the shoots and leaves of one or more species of one aspect (e.g. the prevernal), and by quite other species in another (e.g. the æstival), we must be careful how we refer to these as two different "aspect societies," for we must remember that the underground parts of the species not in evidence on the surface during one aspect are nevertheless present all the time, and may influence the development of the species that happen to be conspicuous at the moment. A society composed of species whose aerial parts vegetate actively in different seasons or "aspects" has been called a "seasonally complementary society." Each case must be decided on its own merits. The criterion of a distinct community is individuality.

CHAPTER IV

The Succession of Vegetation

LIFE never stands still: it is everywhere in a continuous process of flux and change. In the last chapter the units of vegetation were treated as if they were static units, with a definite fixed composition, structure and habit, but in reality they are constantly changing. We must in the first instance define the natural units which are actually formed in the course of the changes of vegetation in order to have something to work on. Broadly, we may regard these units—our associations, consociations and societies—as representing positions of relative equilibrium into which plants group themselves. Some are more stable, others less stable: some, that is to say, remain essentially the same things for a long time, for centuries or perhaps for many thousands of years, others are very transient, giving place in the course of a few seasons to other communities, of different composition. Sometimes change is fluctuating, different species being here to-day, gone to-morrow, and back again the next day, so to speak. This is especially seen in the annual and biennial vegetation of open soil—sandy coasts, roadsides, waste places such as derelict building sites, neglected garden beds, and all ground that has recently been disturbed.

But besides such fluctuating changes there can generally be observed, through a series of years, a definite trend in one direction towards a position of equilibrium. All such progressive change is called *succession.*

We must at the outset distinguish two classes of change which bring about the succession of vegetation. If an area of ground is bare of vegetation, or if new bare ground is formed

—as by emergence of land from the sea, by the drying up of a lake, by deposit of alluvium by a river, by the retreat of a glacier, by a deposit of wind-blown sand, by the fall of talus from a cliff, etc.—plants will, in nearly all cases, begin to occupy it sooner or later. The first species to occupy the area will, however, in most cases give way to others, and these again to others, until a state of relatively stable equilibrium is reached between the vegetation and its habitat. This kind of succession is called the *development of vegetation* (*autogenic succession*), and any particular example is called a *sere*.

But change may also be brought about by continuously acting outside factors which are constantly altering the habitat, thus making it less suitable for the first occupants of the ground and more suitable for others, as for instance a gradual change of climate, the gradual silting up of a lake, the increasing concentration of salt in the soil as an inland sea dries up in an arid climate, the "leaching" (gradual washing out) of soluble salts from the surface layers of a soil by the percolation of rain-water. All these changes, which are independent of the plants, gradually alter the habitat, and thus bring about changes in the vegetation (*allogenic succession*).

In pure *development* the habitat also changes, but it is by the *reaction of the plants upon it*. As the individuals die the products of their decay accumulate as *humus* in the surface layers of soil, altering its physical structure and chemical nature, and increasing its water-holding capacity. Thus the habitat is usually rendered more favourable to plant life, and species which make higher demands on the soil than the original pioneers are able to obtain a footing. In general, bigger plants progressively replace smaller ones; and in all the more favourable climates of the world, on the more favourable soils, woody plants come to occupy the ground, and forest vegetation is ultimately established. As the vegetation becomes closer and taller the shelter increases and provides a habitat for subordinate species which could not enter the earlier communities, so that the eventual forest communities become highly complex.

Of course, these two kinds of change are not necessarily separated in natural successions. Developments are often modified by concurrent changes in external factors. For instance, the development of aquatic reedswamp and fen vegetation on the edge of a lake may be modified by the deposition of silt brought down by streams (41). This can be shown to alter the course of development, i.e. to lead to the formation of communities differing from those which would have appeared if there had been no silting. But it is important to keep clear in the mind the distinction between the two classes of factors (autogenic and allogenic) which influence succession. An instance in which the latter alone is at work is the effect of a gradual continuous change of climate on a plant community. Thus a forest which represents the culminating stage of development for a certain climate at first existing, and is thus in relatively stable equilibrium with its habitat, may alter in composition, or disappear altogether, to be replaced by some other type of community, as the climate becomes, for example, progressively drier or colder.

The early course of development of vegetation on bare ground differs entirely according to the nature of the initial habitat, in the first place whether it is submerged or exposed to the air, and if exposed whether it is wet or dry; for the plants which can colonise such different habitats differ very widely. On submerged ground, as in the shallow water on the edge of a lake or pond, we have the series: submerged aquatic plants, aquatic plants with floating leaves, reedswamp plants. As the soil level is built up by accumulation of plant remains, or by silting, or by both together, till it reaches the surface of the water, fen or marsh will succeed reedswamp. Shrubs and trees which can tolerate water-logged soil round their roots (in this country such trees as alder, willows and birch) often follow, and as the soil level is built higher above the water-level by accumulation of humus, so that the soil becomes drier and better aerated, other trees come in, and the series of communities may be completed by the climatic forest

formation. Such a sere, originating in water, is called a *hydrosere*.

On a dry, bare habitat, such as an exposed rock surface, the talus from cliffs, etc., the early stages are totally different. Lichens and terrestrial algæ, together with rock mosses—plants which can themselves hold rain-water—are the pioneers on bare rock surfaces. These begin to disintegrate the surface of the rock, and with the decayed parts of their own bodies form a thin soil. This is colonised by other mosses which form thicker cushions, and the soil gradually increases enough to support herbs whose roots can do with a thin soil. Then, as the soil grows thicker, more strongly rooting herbs appear, and after a time the seedlings of shrubs and trees take a hold. Eventually, with the thickening layer of soil and humus, comes the climatic forest formation. A sere taking origin on a dry habitat is a *xerosere*, on a rock surface a *lithosere*.

On the talus of cliffs the interstices between the rock fragments form an initial habitat very different from the surfaces of the fragments; and the seeds of herbs, and even of shrubs and trees, often germinate in these interstices and successfully establish themselves at an early stage, long before they can colonise the thin soil formed by the lichens and mosses on the rock surfaces. This depends partly on the weathering of the rock, on how much mineral soil is formed by disintegration and washed down into the interstices, and partly on how much humus is carried down by rain from the surface vegetation. On a talus formed of small fragments—gravel, down to the size of coarse sand—the succession is much quicker and herbs play the leading part as pioneers, binding the loose gravel, forming mats on its surface, and comparatively quickly producing a suitable soil for the establishment of shrub and tree seedlings. On damp sand or silt, such as is laid down by a river in flood, colonisation and succession is still quicker, owing to the relatively favourable soil that is presented to the plants from the outset: herbs or even shrubs and trees begin to colonise the area at once.

The early stages of the development of vegetation thus

differ quite radically according to the nature of the initial habitat, and this influences the course of succession for a considerable time. The *tendency* is always ultimately to develop the most complex community with the largest dominants that the climate permits, whatever that may be, and for this reason such a community is called the *climax community*, because it represents the final pitch of development which the particular climate allows. The complete sere from bare ground to the climax community is called a primary sere or *prisere*.

The climatic climax, or climatic formation, however, as we saw in the last chapter, is not developed on all areas within the corresponding climatic region. The nature of the soil, the presence of permanent bodies of water, above or nearly reaching the ground-level, as well as other local but constant physical factors of various kinds, may altogether prevent it, and so may the existence of a permanent human factor like pasturing or periodic burning. Not only so, but various distinct communities, for example different forest associations or consociations, usually with the same general life form but dominated by distinct species of tree, may develop on different types of soil or under different physiographic conditions, such as marked differences of exposure, within the same climatic area. Each of these forest communities may be in apparent equilibrium with its own particular environment and none may show any tendency to give way to another, so that we must recognise several different climax associations or consociations representing the climatic climax formation ("polyclimax"). This phenomenon must, of course, be distinguished from the arrest or diversion of the succession so that a formation is established quite different from the climatic climax. The community produced by the arrest of the succession in a stage marked by the dominance of a life form clearly "inferior" to that of the climatic climax (for example, grassland or heath instead of forest) has been called a "subclimax." But in a great many cases, probably to some extent in all, the arrest also leads to *deflection* of the sere, producing a community which does not

exactly correspond (though it does correspond in a general way) with any stage of the prisere. This is notably the case where the arresting factor is human intervention, e.g. the regular mowing of fen in the primary hydrosere, or the continuous pasturing of chalk grassland in the xerosere on chalk soil. The "mowing fen" and the chalk pasture are quite distinct stable communities, not identical with any stage in the respective priseres of fen and chalk down. They may be called *plagioclimaxes* (Greek πλάγιος, slanting, sideways) and the short sere which leads to a plagioclimax by deflection of the prisere, may be called a *plagiosere*.

We use the term *climax* for any plant community which is stable in the sense of being in equilibrium with all the existing conditions, of whatever nature, to which it is subjected. In addition to the climatic climax we thus recognise *edaphic* and *biotic* (usually *anthropogenic*) *climaxes*, and many at least of these are, as we have seen, plagioclimaxes.

When a community is not in equilibrium but is a *phase* in development leading to a climax it is a *seral community*. Seral communities corresponding in rank to associations, consociations and societies are often called *associes*, *consocies* and *socies* respectively.

In a country like Great Britain, where man has modified the spontaneous vegetation so that most of it is what we have called "semi-natural," we can rarely find those long series of stages of development from bare habitats to the climatic climax which we have outlined above, and which we can study in regions of the world approximating to the virgin condition. We find instead a patchwork of communities, from the pioneer communities of bare areas to the climatic climaxes, nearly all modified in various ways by man or his animals, and mixed with areas of sown or planted crops. All of these, if left to themselves, would progress towards the climatic climax on the more favourable soils, or to some edaphic climax on special types of soil; but man is constantly stopping or modifying the development or throwing it back to some earlier stage.

Where he has introduced a more or less permanent modifying factor or set of factors, we have biotic (anthropogenic)[1] climaxes or some stage of development towards them.

All development of vegetation initiated, not on new ground, but by some modification or destruction of pre-existing vegetation, is known as SECONDARY SUCCESSION, and it is with secondary successions (*subseres*) that we have mainly to deal in a country like our own. The course of a subsere is necessarily different from that of a prisere on new ground, because the starting-point is different and the time occupied to complete it is less. Instances are the clear felling without replanting of a wood, or the burning of a heath. The subseres most like priseres are those which are started by complete destruction of the original vegetation and its soil, as when stone is quarried or gravel dug, and the gravel pits or quarries are afterwards abandoned. In such cases the original soil is completely destroyed, and the colonisation begins on bare rock or on a loose but purely mineral surface. A parallel case in the water succession (*hydrosere*) is the digging of an artificial pond.

It is obvious that the colonisation of new ground or of bared or partially bared ground must depend on the species of plants available to colonise it. This involves three factors: first, the actual proximity of seed or spore parents; secondly, the means of migration, i.e. the methods by which the seeds or spores are carried (wind, birds, etc.); and thirdly, the suitability of the habitat for the successful germination and establishment of the young plants.

The first colonists of dry areas (terrestrial algæ, lichens, mosses) are widely distributed species whose spores are carried considerable distances by the wind. In a sufficiently damp climate they arrive and establish themselves quickly, in a dry one much more slowly. The herbs which usually come next are frequently annual species, often weeds of waysides and arable land, whose original habitats, before the plants became

[1] Produced by man, from Greek ἄνθρωπος, man, and the root γένω, produce.

"weeds," were just such raw dry soils of the early part of a natural prisere. Such plants often have light seeds, or structures which aid dispersal by wind, such as hairs and plumes attached to the seed or fruit. They form transient communities, which often shift from place to place. The later-arriving perennial herbs appear more gradually, frequently because their means of transport are not so good, so that they come, a few only at a time, at longer intervals. They also commonly germinate more slowly, and require for germination more enduring moisture, so that seeds which arrived too early and fell on the surface of raw soil without humus would not grow into plants.

Finally, many of the trees and shrubs require much more favourable conditions for successful germination and for establishment, especially a deeper soil, so that they have no chance in the conditions of the habitat during the early stages of development (except for instance in the interstices of talus). And here the actual proximity of the seed parents becomes a very important factor in a country like Great Britain, where man has long ago destroyed most of the forest to which its climate is suited. The great distance of adequate numbers of seed parents from many areas which could be colonised by trees if seed were available, combined with the relatively poor means of dispersal of the climax dominants, oak and beech, is sufficient to account for the rarity of natural colonisation of many suitable areas by these trees. Ash and birch have winged fruits, and come quicker over the country generally, while pine, which has winged seeds, often comes very freely if pine woods or plantations are not too distant.

The earlier communities of bare ground are *open*, the individuals scattered here and there with stretches of bare soil between: the habitat is not fully occupied. They consist of comparatively few species, those fitted to cope with the special conditions of life in such situations—the lack of humus, the exposure, the frequent dryness of the surface layers of soil.

The later communities become more and more *closed*

(except where the soil or climate is very unfavourable, in which case the climax, too, remains an open association, as in a desert), the individuals more numerous, and the number of species increases as the habitat becomes more favourable for a greater variety of plants. Certain species become dominant, at first locally; and finally the dominance of a few—often only one or two—is established.[1] The community becomes definitely layered, species which can only exist in good shelter appear in it, and the final structure comes into existence. When this is once established it is difficult for new species to enter the association.

All these features give a definite stable structure to a climax community and contribute to its strong individuality.

[1] In some climax associations, however, for instance many grasslands, the dominance is shared by several species, generally of the same life form. This is called *co-dominance.*

CHAPTER V

Life Forms of Plants

To complete our brief sketch of the nature, structure, and behaviour of vegetation and of the units that may be recognised within it, some further account of the part played by the life forms of the plants composing these units is necessary.

As we have seen (p. 32) the type of plant body, i.e. the life form, of the dominants is the essential character of a plant formation. In other words a formation-type is characterised by the life form of its dominants—the great evergreen leathery-leaved trees of tropical rain forest, the deciduous trees of temperate forests, the grasses of the prairies and steppes, the dwarf shrubs of subtropical deserts, and so on. The characters which have to be taken into account in classifying life forms are those which are of importance in adjusting the plant to its habitat.

One of the most important of all is the nature of the foliage leaves, not only because they are the primary food-producing organs of the green plant, but because it is mainly through the leaves that plants are continually losing water by evaporation to the air, and if they lose water more quickly than it can be supplied from the roots they will dry up and eventually die. The form and structure of leaves are therefore closely related to the prevailing humidity or dryness of the atmosphere in which the plant lives. The drier the air the stronger is its evaporating "pull" on the water in the plant. Leaves may be large or small, thick or thin, of soft or leathery texture, strongly or only slightly protected against rapid evaporation; they may be broad or narrow, or scale-like—or even absent altogether, when their functions are taken over by the stems.

Another fundamental feature of life form is the number and nature of the shoots which the plant produces. Thus we have the forest tree with its bulky woody stem bearing numerous branches raised far above the ground; the shrubs, also woody but much less lofty, and often producing several ascending stems; and the herb, with its comparatively soft body, generally of lower stature still, and showing great variety of construction. Besides these three main categories of flowering plant body, the "lower" plants, such as mosses, liverworts, algæ and fungi show numerous life forms, ranging from the mosses and the giant seaweeds, of very different size but both with comparatively complex structures, to simple microscopic unicellular forms of algæ and fungi. It is with the life forms of flowering plants that we are here mainly concerned.

Herbaceous plants show the greatest variations of life form. Thus we have the simple erect annual plant with a single, or only slightly branched stem, contrasting with the perennial plant, which persists from year to year by means of a stem more or less deeply embedded in the soil. Sometimes this is a compact "rootstock," sometimes a creeping "rhizome." A "rootstock" may produce thin creeping shoots on the surface of the soil (runners) or below the surface (suboles), and both produce fresh plants vegetatively by rooting and sending up aerial shoots at some little distance from the parent rootstock. Then there are the compact underground shoots called tubers, corms and bulbs, which serve the purpose of perennation, and also of vegetative reproduction by the production of detachable lateral buds which grow into new tubers, corms or bulbs.

Finally we have the trees and shrubs which by forming persistent woody aerial stems carry their perennating buds high above the ground.

These various forms of herbaceous or woody plant body, together with the great variety of actual shoots and the numerous types of foliage leaf that have been already mentioned, give rise to a great number of possible combinations and

variations, and several different classifications of life form based on different vegetative features have been proposed. The late Professor Raunkiaer of Copenhagen suggested a classification based on a single principle which has general validity and has proved of great value. This is the position in relation to ground level of the perennating buds which (except in annual plants) give rise to the new shoots and thus carry on the life of the plant from year to year. In most climates there is an annual season unfavourable to plant growth—in hot countries the dry season, in temperate and cold climates the winter. During this season, the great danger is loss of water which cannot be adequately replenished from the soil. Trees and shrubs, whose perennial shoots are raised high into the air, are largely protected against such loss by bark and perennating (winter) buds which are water-proof. Nearer the surface of the soil this danger is considerably less because the air is damper as the result of evaporation from the soil and because the strength of the wind is much diminished. The best protection is obtained, however, if the perennating buds lie on or in the surface layer of soil or are completely buried. Similar protection is afforded to marsh and water plants by the immersion of their perennating buds in water or in subaqueous soil.

Raunkiaer's classification of life forms (p. 237) distinguishes plants with perennating buds borne well above the ground level (broadly trees and shrubs) as *phanerophytes* (Greek φανερός, *phaneros*, visible, exposed). The taller trees, more than 25 feet in height, are *megaphanerophytes* and *mesophanerophytes* (*MM*); trees and shrubs between 6 and 25 feet are *microphanerophytes* (*M*); and shrubs between 10 inches and 6 feet *nanophanerophytes* (*N*) (Latin *nanus*, dwarf). Undershrubs or herbs whose perennating buds are raised into the air, but not more than 10 inches[1] above the surface of the soil, are *chamaephytes* (*Ch*) (Greek χάμαι, on the ground). *Hemicryptophytes* (*H*) (Greek

[1] All these heights are of course arbitrary, but they serve well enough for roughly separating the classes.

ἡμι, half and κρυπτός, hidden) are plants whose buds are formed in the surface of the soil, and *Geophytes* (*G*), those whose perennating buds are buried more deeply and situated on a rootstock, rhizome, corm, bulb or tuber. Finally *therophytes* (*Th*) (Greek θέρος, *thĕros*, summer) are annual plants with a single growing season, but they include "winter annuals" which survive the winter in a vegetative form, often as a short stem with a rosette of leaves, but die after they have flowered and fruited in the next spring or summer. Water and marsh plants, whose perennating buds are situated under water, are called *hydrophytes* and *helophytes* (*HH*) (Greek ἕλος, marsh).

The series *MM*, *M*, *N*, *Ch*, *H*, *G* represents increasing protection of perennating buds as the result of closer approach to and eventual burying in the soil. Immersion in water or in subaqueous soil (*HH*) affords protection to buds comparable with burying in the earth (*G*), and therophytes perennate by means of seeds which are usually more resistant to desiccation than any perennating bud, so that these classes come at the end of the series of increasing protection. Parasites, epiphytes, and stem succulents[1] cannot be brought into this series, but these classes are of no significance in the British flora.

All forest and scrub communities are dominated by phanerophytes, the leaf characters of the dominant trees and shrubs varying widely with the climate; deserts are dominated by nanophanerophytes and chamæphytes (some desert regions by therophytes during the favourable season for vegetation), grasslands by hemicryptophytes, much arctic vegetation by chamæphytes. The life form of the dominants, as we have seen, is the primary character of the great climatic plant formations.

Raunkiaer, however, was specially interested in another

[1] *Parasites* (such as mistletoe, dodder and broomrape) and *Epiphytes* (i.e. plants which live upon the surfaces of other plants but are not parasitic) are put together in a separate class (*E*). In Britain we have no flowering plants which are always epiphytes (such as exist in wet tropical climates) though several species normally rooted in the soil are often found rooted in the humus which collects in the tops of pollard willows, or in the crotches of trees, the latter especially in the damp climates of the west. Plants with succulent stems are also put in a separate class (*S*).

aspect of the distribution of life forms—the percentage distribution of the different classes in the *total flora* of a climatic region. It does not follow that the particular life form represented by the dominants of a climatic formation will also be the preponderating life form in that climatic region. Sometimes it is, as in the region of tropical rain forest where phanerophytes are not only dominant in the rain forest, but also form the great majority of all the species of plants growing in the region. But that is not true of the deciduous summer forest region where phanerophytes are still dominant in the climatic forest formation, but are far outnumbered by hemicryptophytes in the total flora. Raunkiaer showed that what he called the "biological spectrum" of a region, i.e. the list of percentages of the different life-form classes represented in the total flora, was clearly related to the climate.

Most of Britain belongs to the hemicryptophyte climate of north-western Europe: only on the higher mountains do the chamæphytes increase in number till they approach the proportion obtaining in the Arctic regions, while the hemicryptophytes are still very strong. This is because the snow which covers the ground during the long winter serves as a protection to the perennating buds borne close above or on the surface of the soil. These buds rapidly burst into leaf and flower at the beginning of the short growing season when the snow melts and the soil is rapidly warmed and well illuminated during the long hours of daylight.

The life-form classes are also useful in analysing the floristic composition of particular associations and consociations. Forests, the most complex of all plant communities, contain practically all the life forms of land plants (annuals and succulents are rare in them), though the proportions vary according to the climate. Pasture consists almost exclusively of hemicryptophytes with a few geophytes, because buds above the soil level are eaten off. Heaths are characterised by the abundance of evergreen nanophanerophytes and chamæphytes, in relation to the mild winter climate. Permanent heaths are

determined by some factor—climatic, edaphic, or biotic—which prevents the establishment of trees. Communities inhabiting loose and soft soils of all kinds are marked by the abundance of geophytes with widespreading rhizomes or suboles. Therophytes are abundant not only in many deserts but also in all open soil habitats, as in early phases of succession, on sea shores, in waste places, and as weeds in all cultivated land.

Life form is, of course, primarily hereditary, though extremely severe conditions of life may force plants normally belonging to one life form into the class below by the killing off of the upper buds, for example, the wind-cut scrub of nanophanerophytic status, formed on places exposed to violent winds by trees which are micro- or mesophanerophytes in normal conditions. Life form represents the adjustment of the vegetative plant body and life history to the habitat factors, whether this is due entirely to heredity and selection or partly to the direct effect of the conditions of life.

CHAPTER VI

Outline of British Vegetation

AT this point we may usefully introduce a summary outline of existing British vegetation,[1] in order to give the beginner some idea of the material at his disposal.

In Great Britain we have a varied assemblage of plant communities, most of them more or less modified, and many created by man. A certain number, however, notably many of the freshwater communities, the seaweeds, the maritime vegetation of sand dunes, shingle beaches and salt marshes, the vegetation of sea cliffs, and of some of the remoter mountains, moorlands and bogs of the north and west, are but little, if at all, influenced by human agency; that is to say they would have been just the same, as far as we can tell, if man had never inhabited this island. But they are all, whether entirely natural, semi-natural or artificial, open to ecological study, though some will be more fruitful than others.

DECIDUOUS SUMMER FOREST.—The climatic climax of the plains, the valleys and the lower hill slopes of England, Wales and much of Scotland, as well as a large part of Ireland, is the deciduous summer forest formation of Western and Central Europe. In the British Isles it is dominated mainly by one or both of the two deciduous oaks, *Quercus robur* and *Q. sessiliflora*; and on certain soils, especially on the chalk in the south-east and on the Gloucestershire oolites somewhat further north and west, by the beech (*Fagus silvatica*). The beech is now practically confined, as a wood-forming native tree, to the south of

[1] A full account will be found in *The British Islands and their Vegetation* (Cambridge, 1939).

England, though it flourishes, sets seed, and may reproduce itself freely when planted in suitable situations in Scotland and Ireland. On the calcareous soils of the older limestones of the north and west, outside the area of the beech, the woods are dominated by ash (*Fraxinus excelsior*). This ash consociation has not been described outside the British Isles.

The other British trees which dominate widely distributed communities are the alder and the birches (see below). Of markedly gregarious trees the hornbeam (*Carpinus betulus*) plays a certain role in parts of the south-east, the area in which it is certainly indigenous, being even more restricted than that of the beech; and the yew (*Taxus baccata*), with a much wider distribution, is perhaps a climax dominant on some parts of the southern chalk. But both of these trees are better considered as society than as consociation dominants. The hornbeam tends to be subordinate to the oaks, the yew to the beech and sometimes to the oaks.

The native woods have very rarely been left untouched: only small fragments of virgin wood now exist in some of the remoter valleys. Great areas of woodland have long ago been cleared and converted to arable or pasture. Indeed, the proportion of the country occupied by woodland, including plantations, is less than that of any European country except Portugal. In the oakwoods which remain in the south, the shrub-layer, preponderantly of hazel (*Corylus avellana*), with other shrubs associated, is practically always coppiced. A few standard oak trees only are present, not enough to form close canopy; or the coppice is left without standards. Both the oakwoods and the beechwoods of the south have certainly been largely planted, probably in many cases where the particular tree was formerly naturally dominant. Some beechwoods, however, and many oakwoods are almost certainly the direct descendants of natural woods. Natural regeneration of oak and beech wood at present only occurs here and there, so greatly have the natural conditions been altered.

The ash, which reproduces more abundantly and distributes

its fruits more widely than either oak or beech, consequently springs from seed much more often, but where pure ashwood is found within the area of native beech it is generally to be regarded as a seral community or consocies.

The same is true of the birches (*Betula pubescens* and *B. alba*), which, like the ash, are light-demanding trees unable to grow in full competition with oak or beech, and which produce abundant easily scattered tiny winged fruits that readily germinate to give large crops of seedlings. In natural succession the ash commonly precedes the beech, and the birches the oaks, but this rule is not invariable. The actual relations in any given case depend largely on soil preferences—broadly the birches can range over a wide variety of acid, the ash prefers more basic and fresh soils—as well as on distribution factors, and are too complicated to discuss in detail here.

In permanently wet places with neutral or basic soil the alder (*Alnus glutinosa*) appears to be the climax dominant, though it gives way to oak if the soil becomes progressively drier. Associated with it in the succession are the crack willow (*Salix fragilis*), as well as other species of shrubby willows, and also often ash and birch—the former only on neutral or basic soils. Certain alder woods, for instance in the region of the Norfolk Broads, are very probably practically virgin.

As a whole, the British woods (apart from modern plantations of conifers, see p. 25) are semi-natural, that is they are the more or less modified descendants of original natural forest. This statement does not of course imply that there are not many plantations of native deciduous trees. The greater part of these are, however, on the sites of old woodlands, and since the indigenous trees have often been planted, it becomes very difficult, or even impossible in the absence of accurate historical records, to say of any given wood that it is certainly planted or certainly the direct descendant of natural forest. A plantation of the natural dominant on its own soil will in course of time assume most of the characters of a natural wood. (Cf. p. 25).

NORTHERN CONIFEROUS FOREST.—In northern Scotland the

oakwoods begin to thin out and eventually disappear altogether. In certain places both in north and central Scotland there are native woods of the true Scots pine (*Pinus silvestris* var. *scotica*). This region has a climate distinctly different from that of the rest of the British Isles, and is really part of the oceanic division of the region of north European coniferous forests, which are better represented in Norway. Associated with the pine of this region—and indeed far more widespread—are birches, more prolific in small species and varieties than the seral birches of the south. These pine and birch consociations of the north belong therefore to a different formation from the deciduous forests of the south, and their subordinate vegetation is much poorer in species. Many of these are the same as those of the southern woods, the hardier species, which can stand the more severe climate, having penetrated farther north since the retreat of the ice; but the northern woods have also a few species of their own.

The common pine (*P. silvestris*), which is a very widely distributed species in Europe and northern Asia, formed extensive forests in two post-glacial periods. In early post-glacial times the climate of southern England was sub-arctic: later on it became much warmer and forests, sometimes dominated mainly by pine, sometimes mainly by oak, spread over the country. The remains of these forests, largely in the form of pollen grains, are preserved in peat deposits. Probably some of the existing southern pine is descended from these post-glacial pine forests. In the seventeenth and eighteenth centuries the common pine was extensively planted in England, and on the light sandy soils it has in many places spread from the plantations and established itself in pure subspontaneous woods or among the oak and birch, particularly in Hampshire, Surrey, Sussex and Kent.[1] It is interesting to note that in Denmark and Belgium, as in England, there is now no native pine forest, though the species is extensively planted; but in these countries it disappeared only during the historical period.

[1] A great deal of this subspontaneous pine was cleared and used for pit-props during the war of 1914–18, and again during the recent war.

Heath Formation

The heath formation of north-western Europe is developed in wide stretches in western France and throughout the British Isles; also in Jutland, Holland, southern Scandinavia and north-west Germany, mainly on sandy and dry acid soil. The principal consociation is the *Callunetum vulgaris*, dominated by the common ling (*Calluna vulgaris*), which is often pure over considerable areas. The *Ericetum cinereæ*, dominated by the purple or bell heather, *Erica cinerea*, is confined to the western part of Europe. On the serpentine rocks of the Lizard, in Cornwall, and in Brittany, Spain and Portugal, there is a consociation dominated by the handsome mauve-flowered species *Erica vagans*. On some areas the heath association is represented by a consociation of bilberry (*Vaccinium myrtillus*), a deciduous ericaceous under-shrub, which is also often mixed with *Calluna*.

The status of the heath community—its relation to the habitat and to other communities—is different in different places. On exposed high-lying peaty moorland where trees cannot grow, it is often the climatic climax. On sandy soils throughout the British Isles the heath community often occupies the ground, but here it will generally be succeeded by trees, especially birch and pine. Oak and beech sometimes follow, if seed is available. In other places it seems that forest cannot establish itself, on account of the dryness, shallowness, or toxic nature of the soil, though the conditions in question have not been fully worked out. If the soil really stops the succession to forest, the heath community in such cases is an edaphic formation. It is certain, however, that many of our heaths are maintained in this condition not by soil character but by burning and grazing, and here the formation is biotically determined.

Callunetum requires an oceanic or sub-oceanic climate, disappearing as the Continental climate of central and eastern Europe is reached. It cannot grow on some soils, and it does not survive heavy shading, so that it is only dominant in situations and on soils where thick continuous forest cannot become

established. On the other hand it often maintains itself between the trees of a loose birchwood, which does not cast heavy shade. Grazing and trampling destroy it, and, subjected to these conditions, it gives way to certain types of grassland.

Grasslands

The great bulk of the "rough grazings" of Great Britain —excluding land which was formerly arable and has been sown with grass seed ("laid down" to grass)—are partly man-made associations, almost always due to pasturing though not to sowing. The chief exceptions to this origin of uncultivated grassland are certain maritime, sub-maritime, and mountain grass communities where edaphic or climatic factors, especially sea-salt, and violent wind near the sea or at high altitudes, prevent the establishment of woody plants. For the rest it may be said that where grass grows, or rather where most of our meadow grasses grow, trees can grow; and that the cause of their absence is that their seedlings are eaten off and killed, while the dominant grasses of the sward, after being eaten down, constantly shoot again from buds on or in the surface of the soil.

This relation of forest and grassland can be well seen on many of the English grass "commons," which still bear fragments of unfenced woodland. The part of such a common nearest a village, for instance, may be pure grassland. Sometimes it bears isolated bushes or patches of scrub consisting of spiny shrubs (gorse, hawthorn, blackthorn, bramble, briars), which the grazing animals avoid. The grass goes right up to the edge of the wood and between the outlying trees, which cannot regenerate, sometimes because any tree seedlings which became established would be eaten off, sometimes because the compacted soil forms too firm and dry a surface for the seeds of the trees to germinate upon. Thus the area of woodland will constantly shrink and be replaced by pasture.

Within the shade of the wood the grasses of the open common can no longer grow. If the wood is small and the grazing on the

common heavy, few or no woodland species will exist, because the animals come right through it, eating off or trampling down any herbs which appear. But if it is larger and not much entered by grazing animals, woodland plants will be met with as soon as the marginal zone is passed; and young trees may be found where there is sufficient light and the surface soil is suitable for the germination of their seeds.

The actual communities dominated by grasses occurring on such pastured commons vary according to the soil. A widespread association of sandy soil, and of the somewhat similar soils of many northern and western hillsides whose rock is siliceous, is dominated by the common "bent" (*Agrostis tenuis*) and the sheep's fescue (*Festuca ovina*), often with the sweet vernal grass (*Anthoxanthum odoratum*). This is a biotic (grazing) association developed where heath and possibly forest would come if grazing were stopped. If the grazing is less heavy, the heaths (*Calluna* and *Erica*) are often locally or generally dominant. If the soil is distinctly acid and peaty, the wavy hair grass (*Deschampsia flexuosa*) or the mat grass (*Nardus stricta*) becomes prominent or even dominant, and in damper places the purple moor grass (*Molinia cœrulea*) is often dominant.

On heavier and "better" soils with a higher content of soluble bases the common meadow grasses, *Poa pratensis*, *P. trivialis*, *Cynosurus cristatus*, *Lolium perenne*, *Dactylis glomerata*, etc., form good pasture. The corresponding woodland is the pedunculate oak consociation (*Quercetum roboris*). Most of this "meadow grassland" has, however, been laid down to grass, i.e. ploughed and sown, and forms what is called "permanent grass," which is also a "semi-natural" community though of different status from the grassland created by grazing alone. Where there is much lime in the soil the oat-grasses (*Avena pratensis*, *A. pubescens*) and the allied *Trisetum flavescens* often become prominent. On the dry soils of the chalk (and also on the older limestones) we have a closely grazed turf of *Festuca ovina* (sheep's fescue) and *F. rubra*, associated with a number of herbs

characteristic of dry or highly calcareous soils, giving the well-known and highly characteristic association of chalk pasture.

The communities mentioned, or modifications of them, occupy between them the greatest extent of the semi-natural grasslands of Great Britain. Since they are all associations whose form and constitution is determined by grazing, they all give place to something else if grazing is withdrawn. This something else is ultimately forest, provided seed of the appropriate trees is available; but the kinds of shrubs and trees that come, and the conditions under which they come, as well as the corresponding changes in the soil, require much detailed study.

The more porous soils show a general tendency, in our climate, to progressive "leaching," i.e. washing out of soluble salts from the surface layers of the soil, and this frequently leads to increasing acidity of the surface soil with a corresponding gradual change in the vegetation with lapse of time. How far and in exactly what way this external cause of succession affects the development of the vegetation to forest is a question on which we need much fuller information than we possess at present.

Freshwater Communities: Marsh, Fen and Bog ("Moss")

The next group of communities that we must notice are those developed in the succession of vegetation from freshwater to land, which takes place partly by silting and partly by the growth of peat at or near the water-level.

The freshwater communities themselves, consisting partly of algæ (with mosses in some waters) and partly of flowering plants, present peculiar difficulties of classification, and no general satisfactory scheme has yet been produced. The most obvious rough division is into completely submerged plants, plants with floating leaves, and plants with predominantly aerial shoots. We know, however, that the richness or poverty of the water in dissolved oxygen, in various soluble mineral salts, and

also in suspended material (silt), has a determining influence on these communities.

The types of vegetation borne by the alluvial and peat land produced on the edges of freshwater (lakes and rivers) are influenced by the same factors, and we may distinguish between marshland, fenland and bogland according as the soil is formed mainly by silt, by peat containing considerable quantities of lime, or by peat very poor in lime. Marshland may approximate to fenland or to bogland according to the abundance or poverty of lime in the silt, and need not be dealt with here separately.

Fenland occupies the upper parts of the sites of old estuaries as well as the edges of certain lakes and the alluvial soil bordering streams. It is particularly well developed in East Anglia, where the rivers largely drain from the chalk and bring down "hard" waters rich in lime. The greatest area of fenland lies between Cambridge and the Wash, but this is almost wholly drained and cultivated. The smaller area in East Norfolk (the "Broads" region) is in a much more natural state.

The development of fen commonly starts from the reedswamp association, which may be regarded as the culmination of the series of aquatic communities proper. Reedswamp shows consociations of *Scirpus lacustris* (great reed), *Typha* (reedmace) and *Phragmites* (common reed), as well as smaller communities (consociations and societies) of other species, including the tall sedges (*Carex riparia*, *C. pseudo-cyperus*, etc.) and grasses such as *Glyceria maxima* and *Phalaris arundinacea*. As the submerged soil approaches the surface of the water by the continued accumulation of organic debris from the reedswamp plants, the landward edge of the reedswamp is gradually invaded by fen plants, i.e. plants whose shoots are subaerial instead of partly submerged. The two most characteristic fen dominants are *Cladium mariscus*, a stout saw-leaved sedge, and *Juncus obtusiflorus*, the fen rush, though the common reed, *Phragmites communis*, and in some fens *Glyceria* and *Phalaris*, may remain dominant so long as the water-level remains sufficiently high. The two last-named are characteristic of reedswamps and fens,

in which there is abundance of mineral salts in the water. Such fens are also characterised by a greater variety of dicotyledonous flowering plants. The purple moor grass (*Molinia cærulea*) becomes dominant in some fens, as they become drier and especially if the saw sedge is damaged by too frequent mowing.

The fen association, if not regularly cut, is soon colonised by shrubs and trees. Among the shrubs are *Salix cinerea*, *S. repens*, and other willows, *Rhamnus catharticus*, *Frangula alnus*, and the guelder rose (*Viburnum opulus*); and of trees, the birch (*Betula pubescens*), the ash (*Fraxinus excelsior*), and the alder (*Alnus glutinosa*). Ultimately fen wood or "carr" is formed, typically dominated by alder, but sometimes by birch.

Bog, as we have seen, differs from fen because it is developed wherever the water is very poor in basic salts, and it supports a wholly different plant community. Thus it appears on the shores of lakes and pools in a country where the rock is deficient in lime and other basic mineral salts so that the water is markedly "soft." This is well seen in Galway and Mayo in western Ireland where the innumerable lakelets left in depressions after the retreat of the ice are often surrounded by vast areas of bogland. In a very wet climate, like that of western Ireland and western Scotland, this kind of bog covers great stretches of the low country, except where the local drainage is especially good, and is called *blanket bog*. It consists largely of bog moss (*Sphagnum*) and a number of other characteristic plants, many of which, such as cotton grass (*Eriophorum*), deer sedge (*Scirpus cæspitosus*), beak sedge (*Rhynchospora*) and black headed sedge (*Schœnus nigricans*) belong to the sedge family (*Cyperaceæ*). Blanket bogs also cover the elevated plateaux of hill masses such as Dartmoor, the Pennines, and many others in the north and west of Britain and in Ireland, where the climate is very wet. These plateaux are often covered by great sheets of glacial "till" left by the retreating ice, and forming an impermeable substratum to the bog.

Bog may also be developed in fen basins where the climate is not too dry. Bog moss settles down on the fen vegetation

above the level of the "hard" (i.e. lime-containing) ground water, and forms cushions on the fen which are then colonised by other bog plants. The bog moss has a remarkable power of holding water and its cushions can thus grow in height and extend laterally, depending entirely on rain-water. The lateral fusion of the cushions may result in the formation on the surface of the fen of a great lens-shaped bog which grows in height at the centre and whose edges extend so that the bog may come to fill up the whole fen basin. The substance of the lens consists of peat formed by the dead remains of the bog moss and accompanying bog plants, which maintain themselves on the surface as the bog gradually increases in thickness and extent. This kind of bog is called *raised bog*, and its great stretches of reddish brown vegetation are conspicuous features in the fen basins of the great limestone plain of central Ireland. It is upon them that the inhabitants of the central plain have depended for their peat fuel through the centuries. Practically every Irish raised bog has had much peat removed from the edges, but the fact that most of the bogs are still extensive gives an idea of the enormous masses of peat that have been formed. A few raised bogs still exist in northern and western England, Wales and Scotland, but most of the British raised bogs have long ago disappeared as the result of draining and peat cutting.

Blanket and raised bogs are usually colonised by the ling (*Calluna*), but ling does not become dominant while the bog remains wet. If, however, the bog is drained and dries out it usually becomes covered with heath vegetation—often pure Callunetum—and may be invaded by birch or pine, so that birchwood or pinewood is sometimes developed on the dried-out bog peat.

Both blanket and raised bogs are commonly known as "mosses" in the north of England and in southern Scotland whether or not they are dominated by bog moss. "Featherbed Moss" is one characteristic name of a plateau "moss," but most "mosses" are called after localities. In some mosses *Sphagnum* is comparatively infrequent, and they often consist

mainly of great stretches of cottongrass, as on the Pennine plateaux, or of deer sedge, as in the north-west Highlands.

On many gently sloping areas where the soil is not continuously saturated with water the bog dominant is often mixed with bilberry (*Vaccinium myrtillus*) and ling (*Calluna*). Such areas are transitional between bog or "moss" and heath, while on steeper, better drained slopes one of these plants is dominant, sometimes the two together, and we have true upland heath.

On peaty soils six or eight inches thick, overlying siliceous rock, and on the peat debris eroded from the edges of the peat plateaux, the mat grass (*Nardus stricta*) is dominant. On still thinner peaty soils the wavy hair grass (*Deschampsia flexuosa*) often takes its place. A third species, the purple moor grass (*Molinia cærulea*), occurs where the peaty soil is well aerated by percolating (moving) water, and also probably where it obtains a greater supply of bases. *Molinia* frequently occurs also on the damper parts of lowland heaths, and on the edges of mosses as well as on fens.

All this last-named vegetation is characteristic of the country which is called moorland in ordinary English, and associated with wide stretches of heather or bilberry—the upland heaths (e.g. the typical "grouse moors"—Calluneta—of Yorkshire and Scotland). It is distinct from the much wetter bog or "moss," i.e. vegetation on thick wet peat, but the transitional areas in which ling and bilberry are mixed with cottongrass would also be called "moors." The type of grassland (pasture) dominated by *Agrostis tenuis* and *Festuca ovina*, mentioned on page 66, also shows transitions to heath (both upland and lowland) by the coming in of species like *Deschampsia flexuosa* on thin peat or peaty humus, and of the heath plants proper where pasturing is reduced or abandoned. On the slopes of the southern Pennines there is fluctuation between this grassland and upland heath according to the amount of pasturing on the one hand, and on the other the tendency to form peaty humus, which is a constant factor in the moist climate (Adamson, **40**).

The wet climate of the hill country of the north and west of Great Britain leads not only to the leaching of the surface layers of soil owing to heavy rainfall, but also to the building up of acid humus below the herbage owing to the even more important climatic factor of almost constantly moist air combined with low temperatures, which impedes the natural process of humus decay. The result is seen in the prevalence of heath and moor plants in the semi-natural pastures even on well-drained hillsides and even above limestone rock, except where "flushes" from springs or from surface drainage continually bring down fresh supplies of basic salts dissolved from the rocks.

With the exception of the higher-lying and most exposed areas, all these plant communities now occupy country which probably at one time bore forest—at lower altitudes Quercetum sessiliflorae, at higher altitudes Betuletum pubescentis, and at one time Pinetum silvestris. Felling and grazing have been largely responsible for the disappearance of oakwood and its replacement by heath and grassland, thus leading to the general bareness of the hilly regions of the north. Pine rarely spreads from plantations as it does on the drier southern heaths, probably because of the cool damp climate.

The birch and pine woods whose remains are preserved in the peat may be looked upon as the southern extensions, at the higher altitudes, of the birch-pine association of north-central and northern Scotland. A fringe of birchwood still exists in many places above the oakwoods of northern England and southern and central Scotland, but there is hardly any certainly native pine except in Scotland.

Arctic-Alpine Vegetation

While the rounded tops and summit plateaux of the hills whose altitude is round about 2,000 feet are mainly occupied by moor or "moss" communities, many of the higher mountains, especially in the Highlands of Scotland, but to some extent also in North Wales, the Lake District, and Ireland, show

a distinct vegetation generally known as "arctic-alpine." This name is appropriate because the characteristic species are at home in arctic Europe, and some occur also in the European Alps. Arctic-alpine vegetation is found most highly developed and forming varied plant communities on the mountains formed of basic rocks. The summits, ledges and screes of acidic rocks show a few species, but these mountains are generally mainly covered with moor or moss, except where there is bare rock exposed.

All the arctic-alpine *vegetation* lies above the zone of former woodland, though individual *species* may be carried down streams, appearing at lower levels; and some, especially on the Atlantic coasts of Ireland and Scotland, occur at sea-level.

The lowest zone of this vegetation is the so-called arctic-alpine grassland, represented mainly by an association dominated by the viviparous form of the sheep's fescue (*Festuca ovina* forma *vivipara*) and the alpine lady's mantle (*Alchemilla alpina*), with a number of other characteristic species associated. Above the slopes which bear this type of grassland we come to plant communities mainly composed of lichens and mosses, which are by far the most abundant plants of the arctic-alpine vegetation, including many lowland forms, but some confined to the mountains. Here and there we have the sheltered rock faces, ledges and stream-sides which form the habitats of the greater number of the characteristic arctic-alpine species of flowering plants. The individual communities formed by these are generally small, owing to the very uneven nature of the ground, and the study of this varied vegetation is not sufficiently advanced to allow of any useful summary. Finally, we have the summit plateaux with surface composed of loose rocks ("mountain top detritus"), which are a very regular feature of the higher British mountains; and this is occupied by a sparse vegetation of which the shaggy moss *Rhacomitrium lanuginosum* is the most prominent member, often overwhelmingly dominant.

Maritime Vegetation

The last types of vegetation we have to mention are the maritime communities developed on the sea coast, whose habitats are determined by "maritime factors." On the one hand we have the vegetation of blown sea sand forming the well-known coastal dunes (and next to this we may put the closely allied though distinct vegetation of shingle beaches): on the other the very different vegetation of the mud flats (so-called salt marshes), which are covered by the higher tides.

The dominant factor of the sand dunes is the loose, moving sand, not the sea salt, for we find communities of very similar type on blown sand on the shores of freshwater lakes, for instance Lake Michigan in North America. The salt marsh plants, on the contrary, are primarily determined by their periodic immersion in salt water, and by the fact that they are rooted in soil where the water is always more or less salt. These *halophytes* have a peculiar economy, and most of them have more or less succulent leaves.

Dune Succession.—The sandy sea shore in front of the dunes, which is wetted only by the highest spring tides and by spray, is inhabited (where wave erosion is not too great) by a characteristic open community, of which the sea rocket (*Cakile maritima*), the saltwort (*Salsola kali*), the sea sandwort (*Honckenya peploides*), species of orache (*Atriplex*) and the sea couch grass (*Agropyron junceum*) are the most prominent members. All of these withstand a certain amount of immersion in salt water, showing a corresponding tendency to succulence; and all (the last named especially, owing to its habit of growth) arrest the dry sand blown on to them and form low sand hills or dunes through which the plants grow up. The low dunes ("foredunes") formed by *Agropyron junceum* may eventually reach a height out of reach of the spring tides, and this species thus comes to dominate an independent community.

The marram grass (*Ammophila arenaria*) cannot stand prolonged immersion in sea water, but its seedlings freely colonise

the sand just out of reach of the highest tides. The plants have the same marked power of pushing up when covered with sand as *Agropyron junceum*, but they grow much more extensively, so that they form much higher dunes, which they bind and consolidate by the ramifications of their rhizomes and roots. Thus the motion of the surface sand particles is checked, and after a time other species, which cannot colonise moving sand, establish themselves between the plants of the marram. Some of these species are practically confined to sand dunes, but most of them are plants also found in inland habitats. It is to be noted that, contrary to a common impression, the sand of dunes below the air-dried surface is constantly moist, so that sand dune plants get plenty of water.

On dune surfaces protected from the most violent winds, lichens (especially species of *Cladonia*) and mosses (such as *Tortula ruraliformis*), settle down and often become dominant. Various grasses also enter, and often largely dominate, the fixed dune surface. Old grass-covered dunes may form a poor pasture, are often used as rabbit warrens and are the traditional sites of golf links. Scrub is frequently developed upon them. The sea buckthorn (*Hippophaë rhamnoides*) is a characteristic native shrub of some of the east coast dunes, and is very often planted. It is not found wild inland in Great Britain, though it grows abundantly on alluvial gravels in other parts of Europe. Typical heath is developed on some British dunes. Climax forest develops on old dunes in many parts of the world, but not in the poorly wooded British Isles, probably because seed is not available in sufficient quantity. Various trees however (notably species of pine), are successfully planted on dune soil.

SHINGLE BEACH VEGETATION.—Shingle beach vegetation has considerable affinity with that of dunes, many species occurring on both. The smaller shingle is often much mixed with sand, so that the habitats are similar. Shingle is piled above the ordinary high-water level of spring tides by exceptional tides, and on a well-developed shingle beach there is generally a

distinct "storm-crest" marking the last high tide effective in this piling up process. It is on the relatively immobile shingle beyond this crest that vegetation carried down the landward side by the overwash establishes itself, most luxuriantly and characteristically on shingle "spits," rather than on "fringing beaches" which are formed on the edge of the coast and are continuous with the land along their whole length. The plants of shingle beaches are largely derived from and are dependent on the humus of sea drift carried down among the stones.

The vegetation of shingle beaches which are not sandy is characterised by various species of lichens which cover the surface of the stones, and by societies of certain species of flowering plants, among which the sea pea (*Lathyrus maritimus*), the dock *Rumex crispus* var. *trigranulatus*, the sea campion (*Silene maritima*), the horned poppy (*Glaucium luteum*)—the last two also on fixed sand dunes—the purple herb-robert (*Geranium purpureum*), and varieties of the red fescue (*Festuca rubra*) are characteristic species. On old shingle beaches, removed from the direct influence of the sea, an inland vegetation develops, and very often a scrub.

SALT MARSH VEGETATION.—Salt marshes, as already mentioned, bear a characteristic halophilous vegetation in which practically all the species are peculiar to this habitat. The mud (or sand) covered by every tide is too mobile for plant colonisation: it is only the stretches which lie above the high neap tides that are ordinarily covered with vegetation. The "sea grass" (*Zostera*), however, which is well adapted to live submerged for most of its life, is frequently found occupying the flats covered by the neaps, where the race of the tide is not too strong. The glasswort or marsh samphire (*Salicornia herbacea*) is the pioneer on the mud flats,[1] the surface of the mud being often prepared for it by the green alga *Rhizoclonium*. The glasswort is followed by the maritime grass *Glyceria* (sometimes called *Atropis* or *Sclerochloa*) *maritima*. The course of the succession is now very variable according to local conditions, but

[1] Several closely allied annual species of *Salicornia* may be represented.

taken as a whole a mixed vegetation (the general salt marsh community) appears on the flats covered by most of the springs. In this the sea aster (*Aster tripolium*), sea plantain (*Plantago maritima*), sea arrow grass (*Triglochin maritimum*), sea spurrey (*Spergularia marginata*), sea blite (*Suæda maritima*), are general constituents. Two prominent plants, which often become dominant about this level are sea lavender (*Limonium vulgare*) and thrift or sea pink (*Armeria maritima*).

The salt flats covered only by the higher spring tides bear a turf which is a direct result of the closing and consolidation of the general salt marsh community. This is nearly always grazed and is good sheep and cattle pasture, or "saltings," the French *près salés*. The turf is composed of *Glyceria maritima*, or a form of *Festuca rubra*, *with Suæda maritima*, *Armeria maritima*, *Limonium vulgare*, etc. Locally on the south and east coasts of England the shrubby *Suæda fruticosa* occupies a rather special habitat on the edge of shingle beach where this overlies salt marsh. Other species which occur in the various special habitats at the higher levels of the salt marsh are the sea purslane (*Obione portulacoides*, the sea wormwood (*Artemisia maritima*) the stag's horn plantain (*Plantago coronopus*), etc., and locally various species of sea lavender (*Statice*).

The highest levels of the salt marsh, only reached by the very highest spring tides—perhaps only by a few tides twice a year—is often marked by a belt of the sea rush *Juncus maritimus*, and at the same level we find especially such plants as *Glaux maritima*, *Agropyron pungens*, and sometimes other species, such as *Oenanthe lachenalii*, which is also found in brackish marshes. These species do not show the characteristic structural features of halophytes to nearly so great a degree as those occurring at lower levels; mixed with them are ordinary land species, which will tolerate small amounts of salt in the soil.

When the tide is effectively kept out of a salt marsh area and there is adequate drainage by ditches and sluices, the salt is rapidly washed out of the soil and non-halophilous species colonise the area. Excellent pastureland, which can be

converted into arable, is regularly formed in this way. There is no good evidence that salt marsh can develop by the mere accumulation of silt or humus, without human assistance, into a non-maritime vegetation.

We have not aimed in this chapter at giving more than the briefest outline of the nature and general relationships of the chief types of British vegetation. We have necessarily left out of account many plant communities of small extent, such for instance as those of sea cliffs; and also the "artificial" habitats provided by quarries, spoil heaps, roadways and waste places of every description, which are of very diverse rank and status. It was explained in Chapter II that human activity is constantly providing the most varied new habitats, and these become occupied by communities of plants which may be temporary and casual, but may be closely adjusted to their environment, as in all old communities characteristic of habitats of long standing, whether natural or due to human agency. The species of artificial habitats are thus derived from the most various sources, and include weeds and casuals together with certain members of old-established communities which are able to colonise them. For these reasons they often provide good material for close ecological study.

PART III

Methods of Studying Vegetation

CHAPTER VII

Scope and Aims of Ecological Work

BEFORE passing to the actual methods of work, it is well to consider the aims the student should keep in view in undertaking ecological investigation. There is no reason whatever why the work of every intelligent and careful student should not add to the general knowledge as well as to his own, for there are still a vast number of things about our common vegetation that we do not know, many of them not at all recondite. But if the work is to have this result it is essential that the student should know exactly what he is aiming at, and that he should be prepared, if necessary, to revise his aims as the research proceeds.

Every kind of scientific investigation has two stages—the descriptive and the analytical. We must first know clearly what the phenomena are—the things or processes we propose to investigate; and thus we must carefully observe and accurately record before we can proceed to find out how particular phenomena come about. It is the fashion in some quarters to deride "descriptive science," to deny that it is true science at all; but such derision is not in the least justified. Unintelligent

description of badly selected things is worthless, but intelligent description of the right things, undertaken in the right way and with a definite end in view, is not only valuable, it is indispensable to the progress of science.

We should never be content with *mere* description if it is possible to go on to an investigation of causation—of *how things come to happen in the way they do*—for that is the ultimate aim of science. Nor is it at all necessary or desirable to divide our work sharply into two parts, descriptive and analytical, and to finish one before we begin the other. The careful description of some sets of phenomena, for instance of some natural processes, especially if it is quantitative, at once enables us to understand their causes, which we could never have done without it. And even if the problem cannot be solved at once, a careful description will enable us to state it more clearly and precisely, so that we can proceed to the necessary analysis or to experiments in the field or the laboratory.

The scientific description of British plant communities is very far from complete. In one sense, of course, it can never be complete, but there is a good deal that wants doing to improve, and to fill gaps in, the existing general descriptions. A good beginning was made during the first decade of the present century, and the results were recorded in *Types of British Vegetation*, published in 1911. Since that time, for various reasons, the work that has been done has been less systematic, and more largely devoted to special problems. The descriptive knowledge available up to 1939 was brought together in *The British Islands and their Vegetation*, published in that year. The communities that have been distinguished require testing over a wider extent of country than has been actually investigated, in order that the statements made concerning them may be confirmed or modified.

The method of *primary survey* (see Chapter VIII) on which the general classification of associations mainly rests, was to choose a stretch of country and then distinguish and map the communities that could be conveniently represented on

the scale of 1 inch to the mile by means of different colours, modified by stippling and hatching. The first surveyors had, of course, everything to learn. They had to determine the kinds of vegetation which they would select for representation; and later surveyors, besides finding new types in new areas, did not always agree that the original ones were rightly chosen. During the first decade, which we may call "the period of primary survey," the British Vegetation Committee, a small organisation of those actively interested in this work, made an attempt to standardise the colours and symbols used. The scheme drawn up was, however, never published, partly because of the increasing difficulty of securing publication of the coloured primary survey maps, partly because it was felt by some that standardisation was rather premature.

The usefulness of primary survey is certainly not exhausted. It is quite possible to avoid the expense of producing coloured maps by substituting representation in black and white (see Fig. 1, p. 83), though this is not quite so satisfactory as representation in colours. There is no better training in extensive study of vegetation than carrying through the primary survey of a suitable area, because a considerable number of different types are encountered in the course of the work, and the relations of these have to be closely studied in order to represent them properly on a map. There is a good deal to be said for the constant direction of effort to the making of a good map, though this is not, of course, to be regarded as the ultimate goal of any ecological work, which is the understanding of the vegetation studied. But apart from its use to other people, the making of a map focuses effort and compels the student to make up his mind about the status of the vegetation mapped. As we shall see in the next chapter, it is often necessary to "interpret" vegetation, since it is not possible on a small scale to record every plant population exactly as it is, and the necessity of such interpretation is in itself a valuable training.

There is, however, another method of extensive work, which leads perhaps to a deeper understanding of individual plant

communities. This may be called the *monographic method*, and consists in taking a single well-defined plant community, a consociation or an association, such for instance as the oakwood, the heath, or the reedswamp, and following it wherever it is to be found throughout the country, studying the variations of its composition and structure, its dependence upon habitat factors, climatic, edaphic and biotic, and its relations to other communities into which it passes by gradual transitions.

An ideal study of this sort should be extended not only throughout the country but over the whole area of its occurrence in the world; but where this is not possible the monographic method applied within narrower limits will give a deeper insight into the community selected than can be obtained during a general survey of the vegetation of a restricted area.

Both the primary survey and the monographic methods are essentially *extensive*, carried on over a wide area of country, primarily by the methods of observation and comparison. On the other hand, what may be called *intensive* work is concerned rather with detailed investigation of particular problems in one spot. These problems are endless, and may be pursued to any length that the inclination, abilities, opportunities and means at the disposal of the student may dictate. Among them may be mentioned such things as the whole set of problems centring round the *multiplication* and *dispersal* of individual species: the amount of fertile seed a given species produces under different conditions, the actual means by which the species spreads, the rate of spread; the conditions under which germination can occur and establishment of the seedlings take place. Closely linked with these problems are those concerned with *competition* between individual plants, either of the same or of different species: the success or failure of one or the other of two competing species and the actual means thereof, for instance, root competition or overshadowing; the effect upon the result of different conditions of the habitat, for instance, moisture or other properties of the soil. Then

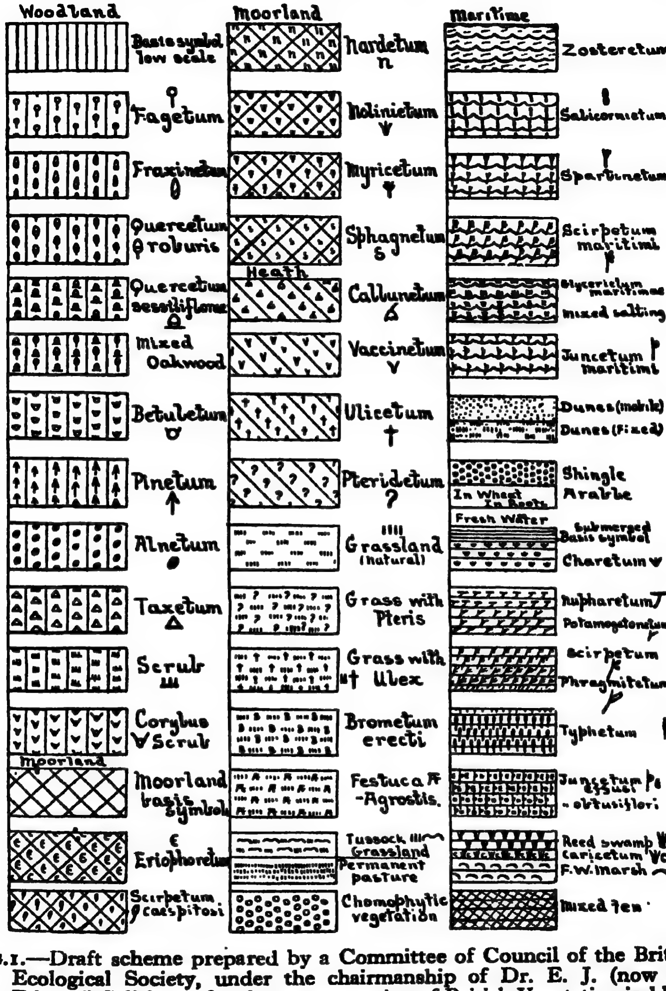


FIG. 1.—Draft scheme prepared by a Committee of Council of the British Ecological Society, under the chairmanship of Dr. E. J. (now Sir Edward) Salisbury, for the representation of British Vegetation in black and white. The scale of the symbols should be varied in accordance with the scale of the map. In general only the "basis symbol," representing the general type of vegetation, should be employed in small scale maps. The other symbols, representing consociation dominants, can be added wherever the scale permits of the separation of consociations. Standardised representation of this kind has many advantages, but should not of course be adhered to where it appears unsuitable. (Reprinted from the *Journal of Ecology*, 8. p. 61, 1920.)

there are the one-sided or mutual *benefits* which plants may confer upon one another, for instance the protection afforded by a larger plant by way of shelter from desiccation, or by a spinose plant in keeping off the attacks of browsing animals; and again the preparation of the soil by the formation of humus from the decaying parts of one plant for the establishment of others; and so on. On the solution of numberless problems of this nature depends the detailed understanding of every case of natural *succession* (see Chapter IV), and some of these, at least, can be studied with every prospect of success by anyone who lives in the country and has time at his disposal.

In working at such problems it is important to employ *experiment* as well as observation, wherever possible. This can be done in the field wherever there is little or no risk of disturbance. It must be admitted that the likelihood of disturbance is a serious drawback to the setting-up of experiments on vegetation in the English countryside. It is often possible, however, to obtain the toleration or even the interest of landowner, farmer or keeper, and thus help to secure the safety of field experiments. And some experiments which do not require apparatus of any sort are quite inconspicuous.

The importance of field experiments in ecology cannot be overestimated. It must not be supposed that experiments necessarily imply instruments or apparatus, elaborate or simple. The experimental method simply means the observation of processes under controlled conditions. The nature and extent of the control necessary are, of course, infinitely various, according to the problem under investigation. For instance, the fencing of a small area against rabbits,[1] the cutting of small, narrow trenches to divert the water supply which ordinarily flows down a slope in a region of heavy rainfall,[2] the supply of extra water to vegetation growing on dry soil[3]—all these are field experiments which have given valuable results. Such experiments are essential for the solution of many eco-

[1] (56) Farrow II, 1916; (97) Tansley, 1922; (159) Watt, Part I, 1923.
[2] (38) Jeffreys III, 1917.
[3] (56) Farrow IV, 1917.

logical problems, and moderate ingenuity will suggest an indefinite number of means of testing the effects of the different factors at work upon vegetation.

Many ecological processes can be conveniently studied in a garden, but it must of course be recognised that the conditions in a garden are very different in many respects from those of natural vegetation, and caution is required in making inferences from one to the other. With this proviso a great deal of information can be obtained from garden experiments. Natural conditions can sometimes be closely imitated by growing plants in competition in boxes filled with the natural soil of their habitats. But such work can never wholly replace observation and experiment in the field.

Something may be said here about quantitative methods. The determination of exact quantitative results from which quantitative laws can be formulated is a well-established method of science. Broadly, we may say that in proportion to the advance of a branch of science its methods become quantitative. This is as true of biology in general and of ecology in particular as of other branches of science. But neither biology in general nor ecology in particular can as yet be treated wholly or even mainly by quantitative methods, though these should be applied wherever they are in place. Quantitative data are not *necessarily* of any value, and we must never make a fetish of them. To be of value for making inferences and ultimately formulating "laws" they must have some kind of *general validity*, i.e. they must either form parts of a general descriptive "picture," or they must be of such a kind that they can be causally related to one another. Isolated data or sets of data which do not fit into a "picture" and cannot be causally related are valueless, or nearly valueless. This is equally true of enumerations of species and frequencies, and of quantitative records of the factors of the habitat, such as soil analyses, evaporimeter readings, light records, and so on. The mere taking of an instrument into the field and making readings, just as the mere recording of the number of individuals of a

species in a given area, is not a virtue in itself and is no guarantee of scientific results. If we would discover causation there must always be a definite object in view, a definite problem to be solved, and observations and records and experiments must always be directed towards solving it. All this may seem very obvious, but it is not infrequently forgotten.

On the other hand, intelligent *qualitative* observation of the constitution and relationships of plant communities, sometimes at once enables us to recognise causes, or at least clearly to state problems for solution. In so far as qualitative observation contributes to a picture of the vegetation of a country or region, it is essential in the first descriptive stage of investigation; a few quantitative data may be added by way of closer characterisation. But it is of little use to multiply these last indefinitely until specific problems arise and can be clearly stated and deliberately attacked.

In attempting to attack a specific problem the best mode of approach should first be carefully thought out. Ecological problems are usually complex, and it may soon appear that the method of attack first chosen is not giving the desired results. One problem leads to another, and it may be necessary to abandon the attempt to solve the first till the second has been stated and explored. The attempt to solve the second may, in its turn, show that a third must first be attacked, and a successful solution of that may cause the first to disappear altogether. For instance, suppose we are trying to explain the puzzling distribution of two or more plant communities over a certain area of ground. At first it may be thought that the undoubted variations in texture and chemical constitution of the soil are responsible. But soil analyses may show that none of these variations can be connected directly with the differences of vegetation. There may appear evidence that these differences correspond, to some extent, with the moisture of the soil, though the communities inhabiting, on the whole, the drier and damper areas respectively are apparently quite capable of growing on either. This suggests a difference in the

incidence of competition between the plants of the two soils, and the difference in competition finally turns out to be determined by the attacks of animals which avoid very wet ground, and bear more hardly on one of the communities which they prefer, thus handicapping it in its struggle with the other, except on the wet ground where it is not so heavily attacked. In the attempt to determine the observed distribution, the original problem, the correlation with soil constitution, has vanished, and the question of moisture has become subordinate to that of competition as affected by animal attack, which thus turns out to be the main cause of the distribution observed. Such a case as this (cf. Farrow, Breckland II, III, IV, and V, see list, p. 243) clearly brings out the necessity of keeping an open mind, and not persisting in a line of attack which is not giving good results.

Also the student should never allow himself to become enslaved by his *methods*. The method which seems most suitable should be carefully thought out beforehand, and strictly adhered to until it is thoroughly tested. But it should be modified or abandoned directly it proves unsatisfactory and a better one can be substituted. Never adhere to routine for the sake of routine. This warning applies particularly to listing, charting and mapping methods (see Chapters VIII and IX). A great deal of valuable time may be wasted, for instance, by adhering to laboriously accurate methods which are giving little information likely to be of value. This is not to say that detailed charting, for instance, in which the position of every individual plant is shown, is not sometimes of essential value. It all depends on the particular object in view.

CHAPTER VIII

Extensive Studies—Reconnaissance and Primary Survey

IT is certainly a sound principle that an extensive study or survey of a fairly large tract of country—primary survey, as it is called—forms the best preliminary to intensive work. Such a survey gives a general knowledge of the types of vegetation and the conditions in which they occur, and enables the student to choose areas or communities for more detailed study with skill and judgment. This advantage is quite apart from the aim of making accurate maps of the vegetation of considerable areas, which is a legitimate and useful end in itself.

RECONNAISSANCE

In the same way the more cursory work known as *reconnaissance* is an almost necessary preliminary to primary survey. In reconnaissance the country is rapidly traversed, the salient features of the vegetation noted and samples here and there are listed, so that the student gets a general idea of what the field is like. Primary survey is a good preliminary, though by no means an essential preliminary, to intensive detailed work, but some sort of previous reconnaissance is practically necessary before primary survey is undertaken.

The first thing to do before starting on reconnaissance is to obtain a good contoured topographical map of the district to be reconnoitred, such as Bartholomew's excellent "layer contour" maps on the scale of half an inch to a mile

(1 : 126,720).[1] or the maps of the Ordnance Survey on the scale of 1 inch to a mile (1 : 63,360),[2] and also, if possible, maps showing the surface geology (which is usually all that matters to the ecologist), for instance, the "drift maps" of the Geological Survey on the same scale, if these are available.[3] From the topographical and geological maps the general nature of the ground and of the soil, the situations of woodland and "wasteland," can be seen in a general way, and the best routes chosen. A bicycle (or motor-car) is a very useful help in working the area quickly, though in the remoter and more sparsely populated districts, where there are few roads, it is often necessary to leave such aids to travel and traverse the country on foot.

Each well-marked type of natural or semi-natural vegetation met with should be rapidly examined, and the dominant and abundant species, as well as any peculiar or striking species, recorded in the notebook. It is best to keep a special notebook for reconnaissance work. At the same time the principal agricultural crops should be recorded. It is convenient and useful to record *on the map itself* (e.g. Bartholomew's half-inch or the large sheet folding maps of the 1-inch Ordnance Survey) the general type of natural vegetation, plantation, arable or pasture land. This can be done by means of symbols, preferably letters denoting the generic names of the dominants of natural vegetation, or in the case of crops the English names. But the method employed must be left to the judgment and convenience of the individual.

A small portable pressing-case for taking home unknown or doubtful plants, a snapshot camera, a trowel, and a tightly stoppered bottle of dilute hydrochloric acid[4] for roughly testing

[1] Price 3s. per sheet, mounted in sections, 4s.

[2] Price of "Popular Edition," each sheet of 27 inches × 18 inches, 2s. od.

[3] Unfortunately, "drift maps" of considerable parts of the British Isles have not yet been published.

[4] E.g. 20 per cent. Note that hydrochloric acid destroys cotton and linen fabrics, but not those made of pure wool. It is almost impossible to avoid occasional drops getting on the outside of the bottle, and from there

the amount of "lime" (calcium carbonate) in the soil, are very useful accessories; but the map, notebook, sharp eyes and a wide-awake mind are the only essentials.

In reconnaissance proper it is important to keep to the *aim* of reconnaissance, i.e. to get a *general* idea of the country and its vegetation, and not to allow the interest to become fixed on particular communities. Primary survey work cannot be done properly on reconnaissance, and time is spent with no satisfactory result if the student lingers too long over one community. At the same time this warning must be interpreted with common sense, for instance if something particularly interesting is met with and there is likely to be no opportunity of revisiting the spot.

It will be obvious to the reader that successful reconnaissance work presupposes at least a moderate knowledge of species and of soils. For the rest it can be carried out with increasing rapidity and increasingly trustworthy results as experience accumulates; but the beginner, if he knows his plants and has some knowledge of rocks and the soils they produce, can obtain useful results.

No attempt should be made in reconnaissance to cover every square mile of the country: that is the business of primary survey. The aim is only a general result based on observation along well-chosen routes, which should traverse all the main types of country in the area. The time necessary to carry out a fairly complete reconnaissance varies greatly with the type of country. Regions with very uniform vegetation, if they are reasonably accessible, occupy far less time than greatly diversified regions, which are always time-consuming in extensive work. In steep, hilly country it is often possible, with a certain amount of experience, to identify, *for recon-*

to the clothes. It is useful to have a rough subjective scale of reactions of soil to hydrochloric acid, e.g. L_0 no bubbles, L_1 few isolated bubbles, L_2 slight general effervescence, L_3 moderate, L_4 strong, L_5 violent. It should be remembered that the surface inch or two of the soil often contains practically no lime, owing to leaching and humus formation, while slightly deeper layers, in which some of the plants are rooted, may contain a considerable percentage.

naissance purposes only, the type of vegetation on an opposite slope from its general appearance at a distance, and in this way much time may be saved. Similarly, good reconnaissance may sometimes be done from the windows of a slowly moving train. It is unnecessary to say that such observation is no *substitute* for actual survey, since many detailed features and local variations will naturally be missed altogether.

Primary Survey

This name is applied to the general method adopted by the first ecologists (Robert and William G. Smith) who began to study British vegetation systematically at the end of the nineteenth century. It was based on the methods of Professor Flahault of Montpellier, and consisted essentially of recognising and describing the larger vegetation units (mainly associations and what we now call consociations), making lists of their floristic composition, studying their relationships and the general nature of their habitats, and recording their distribution in colours on topographical maps of the scale of half an inch or, latterly, of 1 inch to the mile.

The making of the map was an end in itself, though the map might also be regarded as the illustration of the descriptive paper which it accompanied. Such maps, on a uniform scale, and with a uniform system of colouring, have been rightly compared with the series of coloured geological maps issued by the Geological Survey. A series complete for the whole country would present a graphic record of the distribution, not only of the main types of natural and semi-natural vegetation, but also of the principal kinds of cultivated land. This last has to be treated somewhat differently from the native vegetation, since it is impossible to map all the actual crops, if only because they change from year to year in accordance with the system of crop rotation employed. The earliest surveyors in Scotland and the North of England distinguished "upland cultivation with oats" from "lowland cultivation with

wheat" by different shades of yellow, and later surveyors introduced additional types. The shade of yellow represented, however, not only the land actually under wheat, but the whole cultivated area where wheat *could*, presumably, be grown. Eventually it was proposed, by hatching green upon yellow, to indicate the approximate extent of permanent pasture in the farm land, and thus to distinguish, for instance, the Midlands and West of England, where pasture largely preponderated, from East Anglia, where much the greater area is arable. This proposal, certainly a good one, was never carried out, because the publication of the primary survey maps came to an end. Further differentiation of cultivated land could and should be made in mapping areas in which it bulks largely.

The disappearance of any hope of completing a series for the whole country within any reasonable period, partly because of the expense of publication and partly because the interest of ecologists became more concentrated on special problems, together with the facts that the published maps were on different scales (some half an inch, others one inch to the mile), employed to some extent different colours, and appeared in forms not readily accessible to the public, rather seriously detracted from their general usefulness. The primary surveyors, however, did yeoman service to our knowledge of British vegetation. They began the modern systematic study of vegetation in this country, they formed the first organisation for its promotion (the British Vegetation Committee, 1904), and they provided the essential basis for the general treatment published in *Types of British Vegetation* (1911). It may be possible in the future to revive the aim of a complete series of primary survey maps of the vegetation on a uniform scheme if interest in this particular type of work should again be aroused in adequate measure. In the opinion of the author there is no better training in the practical study of vegetation than the work of primary survey, just as there is no better training in field geology than geological mapping.

So long as primary survey depends on the voluntary efforts of single workers, the area chosen by the individual surveyor must generally be determined by its accessibility. Very frequently, of course, it is the area in which the surveyor lives, for much time has necessarily to be spent in the field. Sometimes it may be possible to undertake the survey of an area in which the surveyor spends successive summer holidays. Few people have the means and leisure necessary to make extended visits to remote regions, however interesting they may be. If a choice is available it will clearly fall on a region with much natural and semi-natural vegetation which is striking, diversified and generally interesting; unless indeed the surveyor's interests are predominantly agricultural, when he may choose a region mainly from that point of view. On the whole it is most convenient and useful to take an area coincident with one or more sheets of the 1-inch Ordnance map in preference to a "natural" region bounded for instance by the limits of a geological formation or a river basin. This course involves no waste of space in presentation of the results, and gives more varied data on an equal surface of land. It has the further advantage that the finished sheets will eventually fit together in a complete series for the whole country. An area coinciding with one "large sheet" Ordnance map 27 inches by 18 inches will be amply big enough to begin with. It is always a mistake "to bite off more than you can chew."

Field Equipment and Methods of Work

Field Maps.—These should be the 1-inch and 6-inch Ordnance Survey sheets of the selected area. The maps can be bought direct from the Ordnance Survey Office, Southampton, from Edward Stanford, Ltd., of 12–14, Long Acre, London, W.C.2, or from a local agent. The sheets of the Popular Edition (2s. each) of the 1-inch maps measure 27 by 18 inches, and an unmounted copy may be cut up into eighteen parts, each measuring 4½ inches by 6 inches, and mounted on cards of

the same size.[1] On the backs of the cards should be written the number of the sheet and the number of the section (1–18), and there will also be space for any desirable explanation of the symbols used on the face of the map, and for any necessary general notes referring to the section. This plan is very convenient because each mounted section of the map can be conveniently held in the hand and worked on separately, and several sections can be carried in a canvas or waterproof pocket made for the purpose and measuring say, 6½ inches by 5 inches.

For uniform country like mountain and moorland, and for purely agricultural country the 1-inch map will often suffice, but in varied country where the vegetation changes frequently within a short distance, or wherever details require to be mapped for proper elucidation, 6-inch field maps (1 : 10,560) are necessary. The sheets of these (18 inches by 12 inches, price 2s. each) can be cut into eight sections and mounted on cards of the same size (4½ inches by 6 inches). When no detailed work on the map is required, it is unnecessary to cut them up, and they can be carried whole in a folding leather case. There is no need to buy these 6-inch maps unless and until they are individually required.

NOTEBOOKS AND NOTE-TAKING IN THE FIELD.—Any convenient pocket notebook may be used.[2] The individual surveyor will have his own preferences in regard to the system on which the notes are taken. All that need be said here is that systems of note-taking, as of other things, are very useful so long as they are not slavishly followed when they become

[1] Cards of this size are also useful for mounting blank quadrat charts (see p. 125), and it is convenient to cut or have cut a considerable supply. The advantage of using cards of this size for mounting sections of ordnance maps and quadrat charts is that the card can be comfortably held in the left hand between thumb and little finger while the map or chart is written on in pencil. The dissected, mounted and folded edition of the 1-inch maps, most convenient for the pocket and for general reference, are not at present (1946) obtainable.

[2] Some observers recommend carbon duplicate notebooks, so that they may leave the duplicate at home, and avoid the possibility of loss of the whole season's notes.

unsuitable. The great advantage of following a well-thought-out system is that it tends to completeness of record and ease of reference. One of the commonest experiences of a surveyor of vegetation—and indeed of any worker whose business it is to make records of observations that he cannot immediately repeat at will—is to find, when he comes to write up and think about his notes, that he has omitted to make or to record observations which turn out to be important or even essential for his purpose.[1] A good system will partly prevent such omissions, provided the system is constantly modified and improved in the light of increasing experience. But no system, of course, can be a substitute for the activity of an alert and imaginative mind.

It is always essential to make notes *on the spot* of every fact that is or may be worth recording, with scrupulous emphasis on any fact which runs counter or appears to run counter to a previous conclusion or preconceived opinion. And the records of facts should be accompanied by, but clearly distinguished from, any hypotheses or conjectures that occur on the spot, or later in the day, while the observations are fresh in the mind. The importance of full systematic note-taking and constant consultation and revision of the notes cannot be over-emphasised.

REMAINING FIELD EQUIPMENT.—Map and notebook are the only *essentials* in primary survey, that is to say these are always required, and good primary survey work can on many occasions be done with these alone. But of course no primary survey can be satisfactorily carried through without the frequent use of other articles of equipment. The things that may be necessary or useful are, however, too numerous to carry conveniently on every field excursion, and a selection must usually be made between them. It is a mistake for the average individual to load himself up too heavily with varied impedimenta, because this leads to fatigue and often to inferior

[1] Wet days or "off days" should be used for revising notes, making draft descriptions of the vegetation seen, etc. Gaps in observation thus revealed can be made good at a second visit to the spot.

quality of work. Few people can keep an alert mind when they are tired with carrying a heavy weight. Further, the presence of equipment for too many different kinds of work tends to distract the attention from the general records and problems, for dealing with which it is necessary to keep the mind free for direct observations on the vegetation.

For these reasons it is usually desirable to make observation, recording on the sections of the field map, listing and note-taking, the main objects of the first working over of a section of country; leaving soil testing, or collection of soil samples, light records, photography and other detailed work for a second visit, on which, of course, the first records can be checked and if necessary revised.

It is always well to carry a *pocket flora*, such as *The Botanists' Pocket Book* (Bell, 5s.), for determining doubtful species on the spot. A good *pocket lens* should always be carried by every botanist. The beginner who does not know his species well (and sometimes the more advanced student) will have to take home with him specimens for determination. For this purpose a small, light, *portable pressing-case* that can be slung over the shoulder, *and easily opened without unslinging*, is more compact, and often more convenient than a vasculum. Each plant put in the pressing-case should be labelled when it is collected.

A tightly stoppered bottle of dilute *hydrochloric acid* (see p. 89, footnote 4) is frequently very useful, though it is not wanted on siliceous soils which are known to contain minimal amounts of calcium carbonate. A *measuring rule* (e.g. a carpenter's folding foot-rule) is often useful, and so is a *photographic actinometer* for light records (see p. 158). A *compass*, preferably a prismatic compass, is useful and even necessary in wild country. All the above, together with notebook and sections of maps, can be carried easily enough in a light haversack, or in roomy pockets, without encumbering the surveyor.

A *camera*, on the other hand, *tins for soil samples*, a *strong trowel* for examination of root systems and for collecting soil samples, and a *soil borer* (auger) are relatively bulky, and it is

these which are often better left for particular excursions. Details concerning photography and the study of soils will be found in Chapters XII and XIV. Here it need only be said that a folding roll-film camera may be used by the primary surveyor for snapshots of general views of brightly lighted vegetation,[1] and a few small (i.e. 2- and 4-ounce) tobacco tins are often handy for small soil samples or very small plants which it is desired to take home fresh.

Method of Work in the Field.—In planning a day's primary survey it is important, if time is to be economised, that a fairly close idea of how much ground can be usefully covered should be formed beforehand in order that the route may be appropriately planned. In the first place, it must be borne in mind that the aim of primary survey is to record, and as far as possible to understand, the vegetation of the whole area to be mapped. All the ground must be visited at least once. This does not of course mean that every square yard or even every acre must be examined. At first, before experience of the plant communities to be found in the area under survey has been gained, a great deal more time will have to be spent on recording and listing the species met with than will be necessary later on.

On approaching a particular community it is advisable for the beginner to concentrate attention on a small area which appears to be typical, and to select a spot where the vegetation can be examined in detail, the species present identified, and a short description written. A second and third spot may then be examined in the same way, and the same procedure followed. In this way an accurate idea of the species present and of the structure of the community is gradually built up.

On the preliminary reconnaissance a general idea of the

[1] Really good photography of vegetation is one of the most difficult branches of the art. Experience, of course, teaches what will photograph well and what will not. Broadly speaking, general views with sufficient contrast in *bright* diffuse light are the subjects most likely to be successful with a snapshot camera, but a low sun, giving lateral illumination, though not when the light is orange or red, is often effective. The air should be clear and dry, not misty. See Chapter XII.

broad features of the vegetation will have been formed. One of the first tasks of the survey proper is to determine what plant communities are to be recognised for mapping purposes. These will be primarily associations and consociations of the natural and semi-natural vegetation. Typical samples of these must be thoroughly examined, their species listed and the main features of their structure recorded. The consociations must then be recorded on the sections of the field map by symbols—the initial letter of the generic name of the dominant is convenient—the associations by collections of initials, or other suitable symbols. Boundaries between different consociations or associations must also be drawn, and where there are zones of considerable width, transitional between two communities, these must be marked. Sometimes all this can be done on the 1-inch map, sometimes the 6-inch map will be required.

Many doubts and difficulties will soon appear, largely caused by the modification and fragmentation of the vegetation through human activity. Areas which present too many and bewildering difficulties of interpretation may be roughly described in the field notebook and then left over until further experience has been gained. This will often automatically clear up the difficulties, and then the doubtful areas can be revisited and included in the map. The ideal of recording the vegetation actually on the ground and nothing else cannot always be strictly adhered to. It is quite impossible to represent on a comparatively small scale, such as 1 inch to a mile, all the actual variations met with, whether caused by local variations of habitat or by human interference. The surveyor will soon discover that he is obliged to group many such variations under one type. One of his first tasks is to decide upon the types he will choose in the first instance, but these will very likely have to be modified later on. The notebook should of course contain full notes on the variations, and every effort should be made to discover their causes. These should be dealt with as far as possible in the final description of the area surveyed.

To give an example of what is meant. Suppose a woodland of definite type extends over a certain tract of country. Most of it may be in a stable semi-natural condition, for instance, it may have standards of a certain species of dominant tree, and coppice composed of certain species of shrubs in fairly constant proportions, with a ground vegetation of similarly uniform characteristics. Clearly that tract of country must be represented as uniform, and marked with the initial of the dominant tree representing the consociation, even though it may include areas of a few acres here and there which actually differ from the type more or less widely. The ground may be wet in some places owing to the water-level being close to the surface, and the typical vegetation of the woodland may here be mixed with or replaced by other species which favour wet soil, though such local societies are much too small to show on the map. If a special study of the woodland is being made, they may of course be shown on the 6-inch map, but in any case they must be recorded in the notes. In some places there may be no standards at all, but only coppice of the same general type as where the standards are present. Other areas may be completely replanted with conifers; if these are large enough, they can be indicated by the appropriate initial on the map. In others, again, the wood may have been cleared or partly cleared and left derelict, or cattle may have been allowed to graze through it, causing considerable modification of the vegetation, such as the entrance of many species alien to the woodland and the disappearance of some woodland species.

The detailed recording and study of such effects scarcely belongs to primary survey proper, and it is quite legitimate to lump the whole together as belonging to the typical woodland, when it has quite clearly been derived from this by human agency. In process of time, of course, the site of the original woodland may be converted into something totally different, for instance grassland, or it may be ploughed up and turned into arable fields; and then naturally it can no longer be reckoned as belonging to the original woodland.

Similar cases are provided by the partial drainage of marshes and bogs, by the heavier pasturing of certain tracts of grassland, and so on. These differential treatments may cause very great differences in the vegetation, but the whole area of marsh or grassland is often rightly treated as a unit for primary survey purposes.

A good deal of useful information may be obtained by getting into conversation with woodmen, gamekeepers, farmers or shepherds. It is not advisable to accept all they may say at its face value, but such countrymen can very frequently tell the surveyor relevant facts which he could not easily find out for himself. Experience and observation provide tests which make it possible to sift such information. It is also sometimes possible to get useful data from landowners or their agents or bailiffs about the past treatment of land. Old maps are often very valuable sources of information as to the condition of an area in former times.

Listing of Species.—The making of careful lists of species occurring in the different communities is one of the most important tasks of the primary surveyor, for the actual flora of a plant community is, of course, its essence. It is often not a straightforward matter to make a satisfactory list, because of the modification of the original composition of the community, especially by the entrance of species from outside owing to human interference. Thus one may often find in a coppiced wood a number of species which are not true woodland species, but which enter the wood when it is opened up, either by the agency of wind or because their fruits or seeds are carried there by traffic.[1] Such species are able to establish themselves in the wood because of the light which reaches the ground owing to the absence of a continuous thick tree canopy such as exists in "high forest." Some are distributed through the coppice,

[1] We still know extraordinarily little of the ways in which most species are actually dispersed from place to place, but such evidence as we do possess tends to show that in a populated country they are very largely carried about in the clothes and on the boots of people, in the mud on the hooves of cattle and horses, etc. Men employed in coppicing and felling may carry seeds right through a wood in this way. Other species never get beyond the paths or rides.

others are confined to rides and pathsides.[1] They may have the most various origins, but many of them belong to the class that are often called "marginal," i.e. they are characteristic of the semi-shade of wood margins, hedge banks, etc. Others may be pasture plants or wayside or arable weeds. Similar cases of the collocation of species of very different origins occur in many other modified habitats.

It is not possible for the beginner to distinguish between such different categories of plants, and the only safe course is to make a complete list of all the species which actually occur within the limits of the community; but it is, of course, necessary to add notes when the habitat is clearly modified, and experience will eventually enable the student to assign different species to their proper categories.

When a community is definitely stratified, it is best to list the constituents of the different strata separately. In a wood it is generally quite easy to distinguish the strata (see p. 39), but in some communities, particularly in grassland, the stratification may not be very definite, i.e. the plants may vary greatly in height, and some of the species may bridge the space between two successive strata, expanding their basal leaves, for instance, in one stratum, and their upper leaves in a higher one. It is always well to spend some time studying the phenomena of stratification in such a community, for it is an important structural feature of the community and is of great ecological interest because the actual habitat conditions may differ considerably in the different strata. Well marked societies in which the flora differs distinctly from that of the rest of the consociation or association should also be listed separately.

FREQUENCY SYMBOLS.—Some index of the frequency of each species recorded should be added to its name. It is usual in British lists to employ the following symbols.[2]

[1] This may be a question of dispersal, but the two habitats are different in more than one way, and practically always bear different species and societies.

[2] Some ecologists use a larger number of symbols than those given, but this course is not recommended for the beginner.

d = dominant	*f* = frequent
co-d = co-dominant	*o* = occasional
va = very abundant	*r* = rare
a = abundant	*vr* = very rare

The letter *l* is prefixed to the symbol when the dominance, abundance or frequency is *local* only; thus *la* = locally abundant.

Dominance has reference to a given layer only: thus the pedunculate oak (*Quercus robur*) may be dominant in the tree-layer of a wood, the hazel (*Corylus avellana*) in the shrub-layer, the primrose (*Primula vulgaris*) in the herb-layer, and there may be a moss-layer, in which for instance *Catharinea undulata* or some other species is dominant. When two or more species share the dominance in a given layer, *co-d* (co-dominant) is used, but in some communities there is such a mixture that no species or group of species can be said to be generally dominant. This is particularly the case in seral and all transitional communities.

The assignment of frequency symbols such as those mentioned depends of course upon a subjective judgment without a fixed quantitative standard, such as could be obtained for instance by recording the species occurring within each of a large number of small areas of uniform size (say 1 foot in diameter) taken at random. Hope Simpson (**172**) has shown that subjective estimates of frequency do in fact vary considerably, not only between different observers but between records made at different times by the same observer, particularly in the categories "occasional" and "frequent." Nevertheless subjective estimation is the only practicable method in primary survey and it gives quite useful preliminary data.

It should also be clearly realised that such estimations do and must vary with the size of the area listed. Let us suppose, for example, that an afternoon is spent traversing in different directions a patch of woodland about a mile square, with a uniform flora, that the different species are noted as they are encountered, and that the frequency letters are added from

time to time, and checked and corrected with further observation. An "abundant" species will be one which is never or hardly ever out of sight, a "frequent " species one which is not abundant in this sense, but nevertheless is constantly being met with, an "occasional" species one which is seen perhaps ten to twenty times in the course of the afternoon, while a "rare" species is only seen once or twice. But if now a small area of the wood—say an acre—is thoroughly searched and the species within it noted separately, the species called "rare" in the wood as a whole will probably not be seen at all, even the "occasional" species may not be present in the particular acre, while the species which are "frequent" in the wood as a whole may fall to the rank of "occasional" or even "rare." If, on the other hand, the frequencies of species in a large number of woods of the same general type are considered, the plants which are "rare" or even absent in a particular wood may be appropriately called "occasional" in a wide stretch of country; if a certain number of specimens occur in most of the woods, the "occasional" plants of the single wood may become "frequent," and so on. Thus these terms have a significance which is strictly relative to the size of the area considered, and this fact must always be remembered in compiling lists. The frequency symbols given are most suitable for the larger areas, and when a general account of such an area is being drawn up the number of listed examples of a given association in which they occur, as well as their frequencies within such examples, must be taken into consideration.

SEASONAL CHANGES.—In describing and listing an association or consociation it is very necessary to remember the seasonal change in vegetation. This is most marked in deciduous woods, where there is a very distinct "prevernal" ground vegetation; several species of which, such as *Adoxa moschatellina*, *Anemone nemorosa*, *Scilla nonscripta*, may easily be missed altogether if the wood is visited only in late summer, their leafy shoots often completely disappearing soon after flowering. But it applies to other communities also. The little spring-flowering

annuals ("ephemerals") of open spots in dry grassland (such as fixed sand dunes, etc.) completely disappear in the summer. Many of the orchids of chalk grassland are not to be found in late summer or autumn. On the other hand, heath, fen and salt marsh vegetation do not reach their full development till after midsummer.

Visits should be paid at as many seasons of the year as possible. If only three visits are possible in the year, these should be in April, June and August; if only two, early May and July for woods; if only one, then it should be in late June for woods and grassland (except that which is cut for hay), July or August for heaths and fenland, August or September for salt marsh. These months are suitable for most of England and Wales; in the north and in Scotland, particularly the east, most of the vegetation is from three weeks to a month later in the average year.

Objects of Primary Survey.—The study that can be given to the different plant communities during primary survey is necessarily rather superficial. The main object is to distinguish, record and characterise the larger communities met with and to note their relations to topography, exposure, soil type and ground water. But special note should be taken of the relations of the different communities to one another, of advance or retreat, and of successional phenomena in general—modified, as they are nearly everywhere in this country, or even caused, by the effects of human activity, pasturing of various kinds, drainage, felling, burning, etc. "Marginal phenomena" of vegetation, i.e. modifications brought about, or special communities developed, on the limit between well-marked primary communities by the effect of one upon the other, or by the human factor which has differentiated the two, should always be carefully attended to. It is in the course of observations of these kinds that problems which have to be attacked by more intensive methods of work can be recognised and noted.

The monographic method (p. 82), in which one plant

community, followed over a wide stretch of country—if possible over the whole area of its geographical distribution, which will usually involve visits to other countries—is the centre of interest, can be pursued by methods similar to those of primary survey, but the observations will be more detailed. The habits and behaviour of the dominant and other prominent species of the community will receive special attention, the floristic composition and its variations, the essential features of the habitat, and the relationship to other communities will be closely studied. The life history and behaviour of community dominants is a very important ecological study belonging to the field of autecology. Really thorough knowledge of a community cannot be acquired without close study of the autecology of its dominants.

CHAPTER IX

Surveys of Smaller Areas

In primary survey the vegetation is recorded on existing topographical maps such as the one-inch (1: 63,360) or six-inch (1: 10,560) maps of the Ordnance Survey. Sometimes it is desired to map an area of vegetation—perhaps a quarter-mile across—on a larger scale, say 1: 1,000 or 1: 500. Such a map has to be made *de novo*, and for this purpose the ordinary "chaining" method used in land-survey may be employed. A brief outline applicable to vegetation survey may be given here.

First a convenient *base line* running the length of the area to be mapped must be selected. Every part of this should, if possible, be visible from every other part. The two ends are marked with permanent pegs. It is of the first importance to get the base line *straight*. This is done by planting light wands or rods about 5 feet long at the two ends and then "ranging" these with a series of other rods, at intervals of (say) 100 feet, till all are seen to be exactly in a line. Standing at one rod and looking towards the other end of the line the next rod should completely hide all the others. A second worker goes to each rod in turn and adjusts its position in accordance with the signals (by hand waving) of the observer. When the line is perfectly straight, it is carefully "chained," i.e. measured with a surveyor's chain or tape,[1] and permanent pegs driven at 100-foot intervals.

[1] 100-foot and 50-foot tapes are much more convenient and lighter to carry than chains, but they stretch and shrink, sometimes considerably, if they are wetted. They should therefore be protected from rain as much as possible, and checked against a standard at intervals.

The base line having been thus fixed and measured, *perpendiculars* are erected upon it at suitable intervals, extending to the edges of the area to be mapped. These should be located where they will run *across* the greatest number of physical features (if present) and vegetation boundaries. The right angles can be determined either with the *cross staff* or with the *optical square*.

The *cross staff* is planted in the ground on the base line at the point from which a perpendicular is to be run: on its top (at the eye-level) fits a hollow iron prism (cross staff head) of octagonal section, in the sides of which are vertical slits. A very narrow slit in one face is diametrically opposite to a broader slit with a vertically running thread in the centre. The head is turned so that on looking through the narrow slit the wire in the opposite slit falls exactly on a vertical rod planted further up the base line. The observer then looks through the narrow slit at right angles to the one falling on the base line, and a rod is stuck in the ground in the direction of the perpendicular; this must be erected so that it coincides with the wire in the opposite slit. The line joining the cross staff and the rod which falls on the second wire is then perpendicular to the base line.

The *optical square* (which makes a cross staff unnecessary, and is only very slightly more difficult to use) is a hollow cylinder pierced by three openings, two large and rectangular, of different sizes and at right angles to one another, and a small circular eyehole diametrically opposite to the smaller rectangular opening. When the instrument is held horizontally (the observer standing on the base line and looking down it through the eyehole) a vertical rod planted on the base line will be seen in the upper part of the field of vision. The lower part of the field is cut off by a block from direct vision, but by means of a mirror at 45 degrees to the line of vision images of objects in a line at right angles to the line of vision are reflected in the lower part of the field. Thus a rod seen in the lower part of the field and falling in a vertical line with the rod on the base line

seen in the upper part will be on a perpendicular to the base line drawn from the position of the observer.

The perpendicular, determined either with the cross staff or with the optical square, is then ranged and measured with a chain or tape, and its length recorded. Each perpendicular so made is designated by its distance from the end (origin) of the base line, e.g. 148 feet in Fig. 2. Secondary perpendiculars (offsets) are then erected on the primary ones in the same way, at suitable intervals, where they will "pick up" (i.e. cross) the largest number of "features" (i.e. physical or vegetational boundaries), and these offsets are recorded in a notebook[1] under the primary perpendiculars to which they belong, each being designated by its distance from the origin of its primary perpendicular, e.g. 39 feet in Fig. 2. The "features" or boundaries crossed by the base line itself are recorded separately in the notebook, with the distance of each from the origin of the base line (Fig. 2).

The data are now complete, and all that remains is to make the map. The base line, perpendiculars, and offsets are drawn to scale on a sheet of paper of the necessary size, the features on each line put in, and then joined up with those on adjacent lines. If the perpendiculars and offsets are sufficiently numerous and have been suitably located, the making of the map will be a straightforward, almost a mechanical job; but should there remain doubt as to certain details, the map may be taken into the field (on a drawing-board) and the boundaries completed by eye on the spot.

When plant communities to be mapped are sharply defined and their boundaries not too complicated, the method described above is the best and quickest. But if a great number of communities of complex distribution have to be mapped, the "method of squares" is better. In this, instead of independent perpendiculars and offsets, a complete system of squares cover-

[1] A "surveyor's" or "reporter's" notebook (opening at the end instead of the side) is convenient for this purpose. Two parallel lines, between which the distances are entered, run the length of each page, in the centre, and the data are recorded from the *end* of the notebook, i.e. beginning at the last page and working upwards from the bottom of each page.

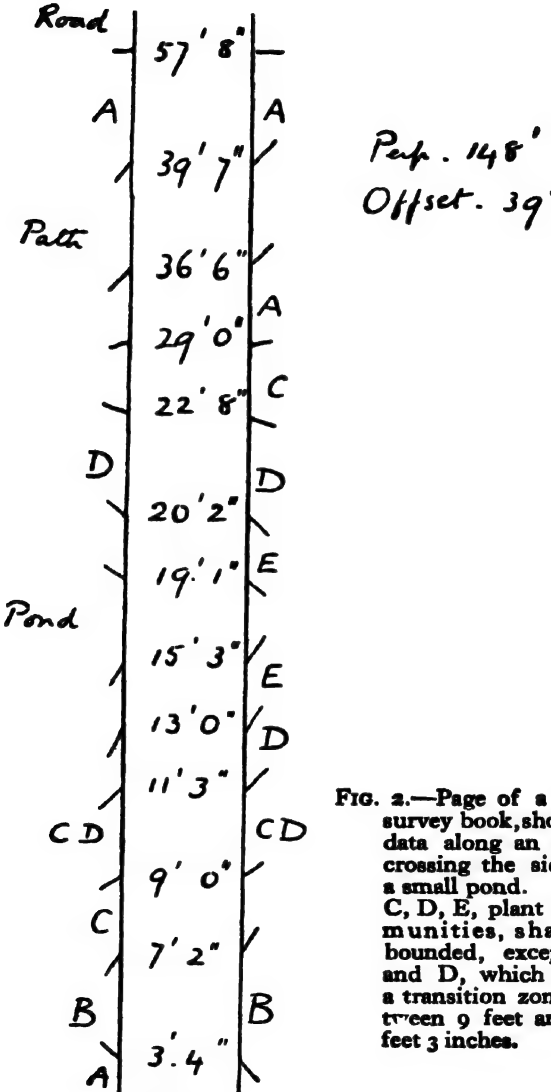


FIG. 2.—Page of a field survey book, showing data along an offset crossing the side of a small pond. A, B, C, D, E, plant communities, sharply bounded, except C and D, which show a transition zone between 9 feet and 11 feet 3 inches.

ing the area to be mapped is erected on the base line. The side of each square is of any convenient size (say 100 feet, 50 feet or less), and the corners are marked by planting light rods. The right angles are determined as before, but once this has been done and the first squares constructed, any required number of squares can be quickly made by "chaining" the 100-foot intervals along two perpendiculars and "ranging" the remaining corner rods in the two directions, i.e. parallel to and at right angles to the base line. In this method each square is mapped separately on squared paper, and should not be too large to map by eye with reasonable accuracy. In the case of larger squares a little assistance from an observer on the side of the square armed with a light 5-foot measuring rod, and perhaps an optical square, to give the recorder his position in the square, is helpful. A little practice will soon enable workers to adapt their procedure to the special case.[1]

The methods of survey described above require at least two workers; and a third, to fetch, carry and do odd jobs, is desirable. After the base line has been chosen, ranged and measured, different parties can work at once on different parts of the area, and in this way, after a little experience, and with sufficient equipment in the way of rods and tapes, a considerable area can be surveyed in the course of an afternoon. It is of course essential that independently working parties should have careful and identical instructions as to the exact method of work, the symbols to be used, and so on, in order that the records may be uniform and sufficiently complete.

The whole of the vegetation should be carefully examined before the survey is started (a previous afternoon should generally be devoted to this), even when the species are known, and a workable scheme of the communities to be recognised decided upon. It is a mistake to erect more perpendiculars and offsets,

[1] A detailed description of surveying vegetation by the method of squares is given by McLean & Cook (*Practical Field Ecology*, Chapters III and IV), but they use it for smaller areas to be mapped on a larger scale, e.g. a base line of 150 feet with squares 10 feet wide to be mapped on a scale of 1:120. The lay-out of the squares is described by the authors as a "grid" (Cf. Chapter X).

or squares, than can be comfortably disposed of in the available time. The work should never be hurried at the beginning. Combined quickness and accuracy come with practice. It is rarely advisable (except on private ground) to leave planted rods out overnight, but if the area cannot be completed on one occasion the perpendiculars for the unfinished part of the work can be quickly constructed if permanent pegs (flush or nearly flush with the ground) have been driven at the 100-foot intervals along the base line.

It is rarely worth while to map a very large area in any great detail. The process becomes wearisome and does not repay the time and labour spent upon it. It is much better to spend the time on detailed ("quadrat" or "grid") study of small selected portions, or on a transect across zoned vegetation.[1] To this detailed work a more general map of the whole area may be added if this should seem desirable. For this the 1:2,500 Ordnance map may suffice as a basis, or a special survey on the lines described may be carried out. In a senior school class opportunities may thus be found for exercise of the different interests and aptitudes of the members. The survey work is, of course, an excellent exercise in practical geography, and the combination of this with vegetation study should be welcomed by teachers. The whole of the work described, as well as the transect and quadrat work dealt with in the next chapter, is in the highest degree educational, evoking and training the powers of observation and encouraging accuracy, quickness and ingenuity, as well as bringing the student into the closest touch with nature.

[1] See Chapter X.

CHAPTER X

Intensive Studies—Large Scale Charts of Vegetation

When we turn from extensive to intensive ecological work, we begin to come to grips with the detailed problems of vegetation, which cannot be solved by extensive work. Primary survey or the monographing on extensive lines of a given type of plant community over a wide area is largely a geographical study, concerned with the distribution and broad features of the larger units of vegetation. To get to the bottom of the structure and development of individual communities, to learn how it is that particular species become dominant or abundant in some places and not in others, to understand the mutual relations of species, the weapons with which they fight, the advantages they may confer on each other, their reactions to different factors of the habitat, the limits of their tolerance of varying conditions, we must concentrate our attention on particular problems and employ the most various means for their solution. In this field of work, most particularly, elasticity of mind, lively imagination and ingenuity in devising methods of attack, are essential, in addition of course to the always indispensable determination and persistence.

In dealing with primary survey one can describe fairly closely the necessary programme of work, but with intensive work it is impossible to do anything of the kind: because the problems are so various and because they often differ according to the community studied, no fixed procedure can be laid down. We shall, therefore, describe in turn some of the methods that

may be employed in studying first the vegetation itself and secondly the habitat. The particular methods chosen by the student must depend on the particular vegetation to be studied and on the particular problems he can formulate in regard to it. Further, it must be remembered that ecological technique is still in an early stage of development, so that there is ample room for new methods of work and for improvement and adaptation of existing ones.

Every genuine original worker in science is an explorer who is continually meeting fresh things and fresh situations to which he has to adapt his material and mental equipment. This is conspicuously true of our subject, and is one of the greatest attractions of ecology to the student who is at once eager, imaginative and determined. To the lover of prescribed routine methods with the certainty of "safe" results the study of ecology is not to be recommended.

Since this is a book intended for the beginner, methods which involve any considerable special training are not described. If the investigation of certain ecological problems is to be carried far, the use of such methods cannot ultimately be avoided. The keen student who finds them necessary will be willing and able to train himself to use them. Here the emphasis is laid on problems which need only simple methods, and which are often neglected, partly owing to the excessive prominence of the laboratory in modern botany. Comprehension of much of the behaviour of vegetation, which we still grasp very incompletely, depends on the solutions of these simpler problems, which require only the simplest material aids.

Large Scale Charts of Vegetation

An essential aid to the investigation and recording of vegetational data, though always to be used with discrimination and forethought, is the making of vegetation charts.

Vegetation Charts represent the details of the vegetation of a small area on a large scale, and are constructed *de novo.*

They are conveniently distinguished from *vegetation maps*, which are either constructed from pre-existing topographical maps by plotting the broad vegetational features on the topographical map as a basis, as in the coloured maps of the British "primary survey" (Chapter VIII), or by making a new map by the methods of land survey (Chapter IX).

It was explained in Chapter VIII that the making of a vegetation map which forms part of a uniform series that could be extended to cover the whole country can be regarded as an end in itself, apart from the knowledge acquired and the experience and training afforded by the process of making the map. This is not usually the case with the vegetation chart, which should not be made for its own sake, but only as a characteristic sample of the detailed structure of a widely distributed typical community, to illustrate some striking distribution of vegetation in relation to habitat, or (and this is the most important use of charts) as a definite aid to the solution of a definite problem.

Many striking distributions of plants are observed from time to time in the field—for instance, aggregations of one species around or among individuals of another, the growth of a species or a community only in positions exposed to or protected from the sun or the wind, the regular zonation of vegetation round a pond or lake, or again round a hillock or on the two sides of a ridge. Very often such features can be sufficiently dealt with by descriptive notes alone or rough charts drawn by eye; an accurate chart to scale would not repay the time spent upon it. But in other cases the interest of the distribution and the accuracy with which it follows habitat conditions, which can often be separately determined and charted, seem to demand an exact chart, and the close observation required for this purpose may reveal the existence of other factors not at first suspected, or may show that the supposed correlation with habitat, which seemed obvious, breaks down. The judgment required for a correct decision grows of course with experience in ecological work.

As a means to the investigation of a definite problem charts are often indispensable. This applies especially to the study of succession or change in vegetation from year to year. The chart then becomes a record or datum with which future records can be compared; and only with their help can succession be accurately and quantitatively studied. We may often *infer* succession by comparing pieces of vegetation and concluding that one represents a later phase into which another will in course of time develop. When a number of obvious transition phases are available, such inferences have a high degree of probability, and most descriptions of successions have in fact been based on this kind of evidence. But at the best these inferences are not so satisfactory as direct observation on the same piece of ground. A succession which is directly traced has a certainty that cannot be impugned, the time required is discovered, the exact details are followed, and the causes of succession are often automatically revealed. The drawback is, of course, that such direct study of succession has to be extended over several or many years; some successions occupy far more than the span of a lifetime. This difficulty may be partly met by choosing different stages of an inferred succession, as represented in different places, and studying each separately by means of a series of charts taken at intervals of time. In this way, if the supposed succession is a real one, the records may be continued until the last chart of one series corresponds with the first of another, and the whole may thus be pieced together.

Methods of Charting on Different Scales[1]

The Grid Method.—This was first successfully employed many years ago by a party of students under Prof. F. W.

[1] There is a certain advantage in keeping to the decimal (metric) system of measurement, particularly in the largest scale charts (1 : 10, etc.), which can be plotted on millimetre squared paper. But the practical convenience of using the common English duodecimal system for smaller scale charts (e.g. 1 : 60 or 1 inch to 5 feet), may outweigh the advantages of decimal uniformity.

Oliver on a very gently undulating salt marsh in Brittany, certain interesting areas of which it was desired to chart on a large scale (1 : 60). The method is only useful where the boundaries of small, well-defined, uniform communities can be drawn.

A square (or system of connected squares) is laid down with sides of 25 feet. The corners of isolated squares or systems which will be wanted for future re-charting must be marked

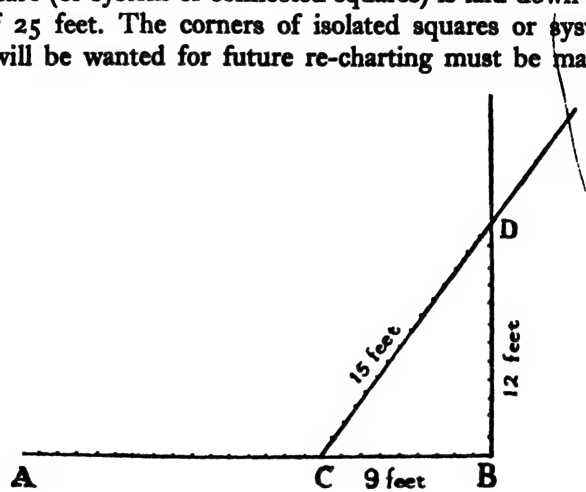


FIG. 3.—Method of determining a right angle on the ground. (See text, p. 117.)

by permanent pegs. Iron or seasoned creosoted hard wood pegs driven in flush with the soil surface are necessary; soft wood pegs rot quickly, and may disappear altogether in a year or two. If there is likely to be any difficulty in finding the pegs on a future occasion, the exact location of one at least of the pegs must be fixed by measurement from two permanent objects in the neighbourhood. Much time may be wasted in trying to find the corner pegs of an old square if such precautions are neglected.

When two corner pegs at each end of one side (base) of the grid have been fixed and a 25-foot tape run between them,

a second tape is run from one peg perpendicular to the first. The right angle may be determined by means of a cross staff or optical square,[1] or if these are not available the right angle can be fixed by the following method (Fig. 3).

If AB is the base of the grid and a right angle is to be con-

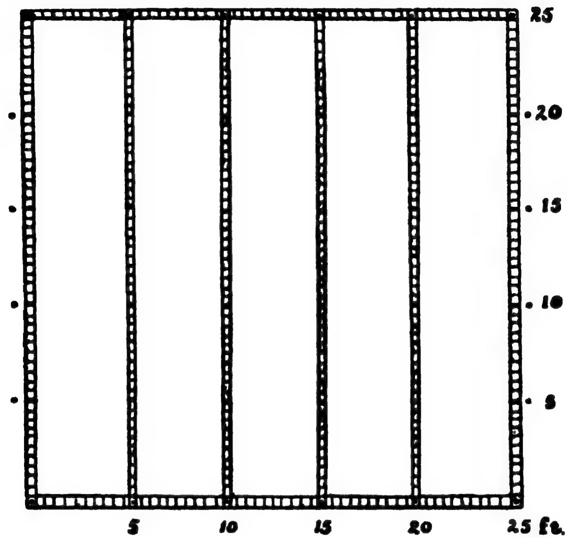


FIG. 4.—Diagram of grid tapes as laid out on the ground. The scale of the figure is 1 : 120, or ½ inch to 5 feet. The chart should be made on double this scale (1 : 60, or 1 inch to 5 feet).

structed at B, slip the metal loop of a measuring tape on an arrow[2] at B and run out the tape approximately at right angles in the direction BD. Now slip the loop of another tape on an arrow at C, 9 feet from B along BA, and run out in the direction CD. Rotate the tapes BD and CD about B and C respectively until the 15-foot mark on CD coincides with the 12-foot mark on BD. Fix this point (D) with an arrow. The angle ABD (CBD) is now a right angle. When the square has been

[1] See Chapter IX, p. 107.
[2] Land survey "arrow": ordinary meat skewers serve equally well.

measured out and the corner pegs inserted, the measuring tapes may be replaced by ordinary tapes marked in any convenient conspicuous way at foot intervals and thin stakes stuck in the ground at 5-foot intervals. Four cross tapes also marked at foot and more conspicuously at 5-foot intervals are

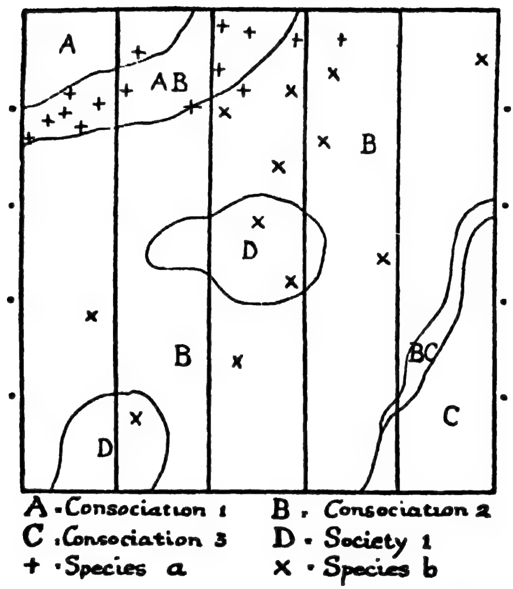


FIG. 5.—Grid chart on a scale of 1 : 120 (actual charts should be on twice this scale). The three consociations (A, B, C) and their transitions, also two examples of a society (D), are separated by lines, and marked by capital letters (in actual charts these should be the initials of the genera, see p. 104). Vertical and diagonal crosses mark the positions of large isolated individuals of two species. Cf. Fig. 5.

then run parallel with two of the sides, dividing the square into five strips as with the bars of a gridiron (Fig. 4). The grid tapes should run *across* the maximum number of community boundaries.

The grid is now ready to be charted on squared paper ruled in inches (5 feet on the ground) and tenths of an inch (6 inches

on the ground).[1] A square with 5-inch sides and the grid lines at 1-inch intervals is ruled off in pencil on the paper, and the charting, which can be done by one person working alone, is proceeded with. The boundaries of the communities are easily and rapidly drawn in pencil. The names of the communities

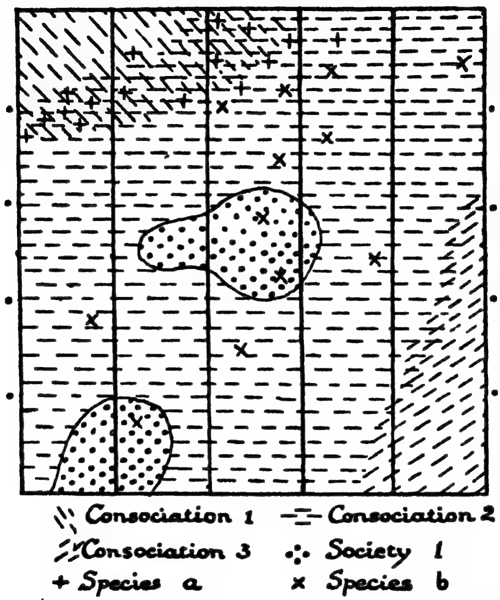


FIG. 6.—Grid chart on a scale of 1 : 120 (actual charts should be twice this size). The consociations and their transitions are represented by interrupted diagonal and horizontal lines, two examples of a society by dots. Vertical and diagonal crosses mark the positions of large isolated individuals of two species. Cf. Fig. 5.

are written in large initial letters (of the dominant genera) on the corresponding areas (Fig. 5). If preferred, the areas may be marked by interrupted lines drawn in different directions. This has the advantage that transitional areas can be easily shown by the overlapping of two sets of lines (Fig. 6). The positions of any isolated large plants can be marked by con-

[1] Books ruled in these dimensions are readily obtained at any good stationers.

venient symbols (Figs. 5 and 6). The boundaries of communities, symbols, etc., should afterwards be inked over and the chart kept for reference. Charting on this scale should be accurate to 3 inches or less on the ground.

If the metric system is preferred, a smaller grid, 5 metres square, may be employed and charted (scale 1 : 50) on a square decimetre of millimetre squared paper mounted at one end of a card 6 inches by 4½ inches as shown in Fig. 9 (p. 126).

It must again be emphasised that the grid method is only suitable for charting the distribution of sharply bounded communities on fairly level ground, and fixing the approximate positions of large isolated individual plants. It may be used for illustrating samples of a vegetation showing these characters, for succession studies, and where the distribution of the small communities can be correlated with some physical factor, such as soil water content, or (in a marsh or fen) depth of water-level below the soil surface.[1]

Charts showing all individual plants have of course to be on a much larger scale—not less than 1 : 10 (see below, p. 125). In such charts it is best to use as symbols for marking each individual plant the initial letter of its generic name, and when two or more species of one genus are present to add the initial (small) letter of the specific name in each case. If two or more genera with the same initial are present, a later characteristic letter of the name of all but one must be added. Thus E.c. = *Erica cinerea*, E.t. = *Erica tetralix*, and again S. = *Sanicula europea*, Sc. = *Scilla non-scripta*. The symbols used must always be clearly explained at the bottom or on the back of the chart.

THE TRANSECT.—This is the name given to a line or belt of vegetation selected for charting. The scale is in general larger

[1] A very full description of charting vegetation on a comparable scale (e.g. 1 : 120) by the method of squares, which they call the "grid method," is given in McLean and Ivimey Cook's *Practical Field Ecology*, in Chapters 3 and 4, and of levelling a grid in Chapter 5. In this book the term "grid" is used for a square across which tapes are laid in one direction only, like the bars of a gridiron.

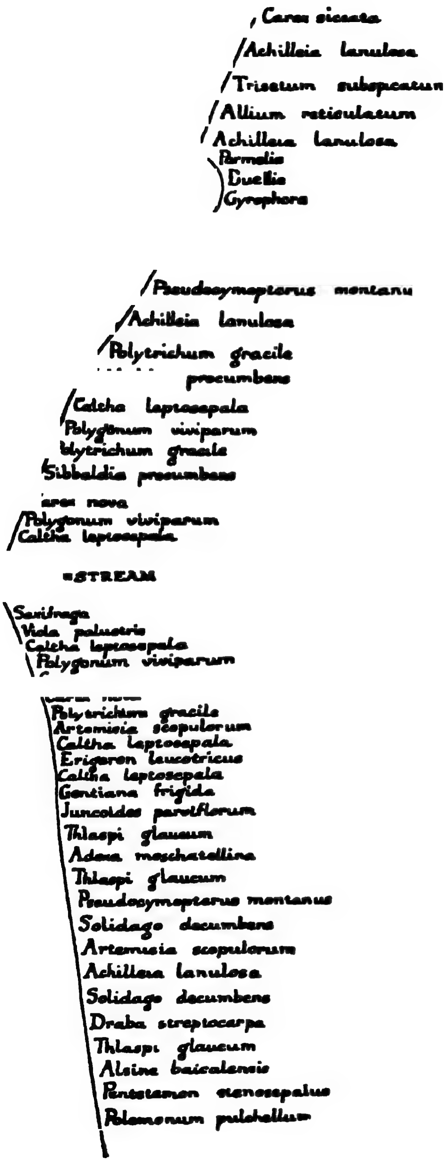


FIG. 7.—Line transect chart across the valley of a small stream in the Rocky Mountains of Colorado. The chart represents the individual plants of the field and ground layers of the pine-spruce forest touching the transect tape, which follows the line of greatest slope. A series of eight to eleven plants on each side of the stream belong to the stream-side community. No single species is dominant in the field layer. (After F. E. Clements.)

than that of the grid chart, and the individual plants are shown by appropriate symbols. The transect is particularly useful when the vegetation is *zoned*, i.e. when it forms more or less regular successive zones representing different communities. Zoning may be in relation to a regular change in physical factors of the habitat (e.g. decreasing water content as we pass outwards from the edge of a lake) along the line perpendicular to the extension of the zones. Again, it may indicate a progressive invasion of plants into a seral community from one side, without perceptible change in the habitat. The transect is made at right angles to the zones, i.e. in the direction in which the habitat factors show the maximum change, or in the direction in which invasion is proceeding.

The advantage of a transect chart is that it shows a definite *range* of vegetation, and by re-charting the transect at suitable intervals of time any progressive change in the vegetation along the line of the transect can be detected and measured.

THE LINE TRANSECT (Fig. 7).—This is the simplest and quickest form of transect to chart. It is made by running a measuring tape along the desired line, and marking the positions of the individual plants touching the tape on one or both sides, writing their names or the appropriate symbols on one or both sides of a corresponding line drawn on a page of squared paper, or on a square decimetre mounted on card (see above, under grid method). Several sections of the same transect can, of course, be plotted side by side on the same page or card.

With regard to the scale of the transect chart this must vary according to the size of the individual plants and the closeness of the vegetation. If it is only desired to record the individual trees and shrubs in a wood, for instance, 1 : 50 or even 1 : 100 may be a large enough scale. If we are dealing with herbaceous vegetation, 1 : 10 is very often suitable, except where the plants are very small, for instance crowded annuals springing from seed on fallow soil or on certain areas of salt marsh, and here a scale of 1 : 5, or even 1 : 2 or 1 : 1, may be necessary.

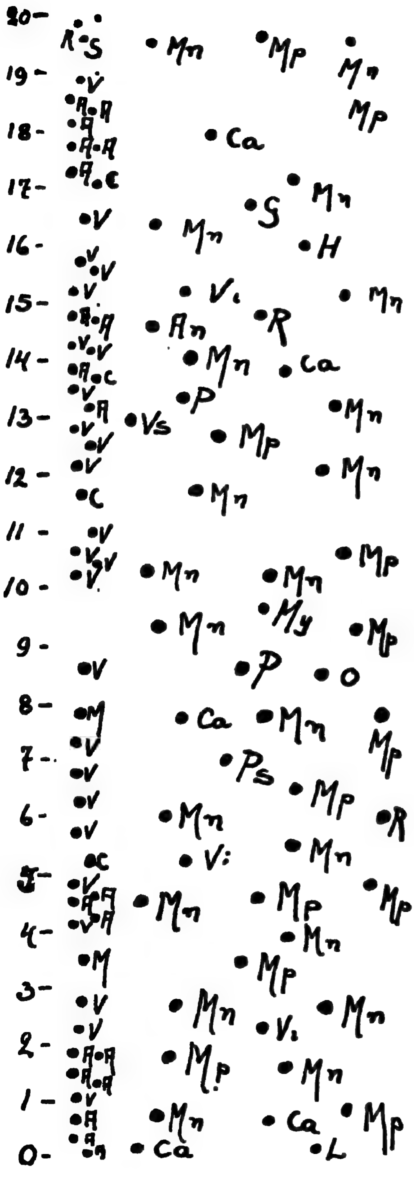


FIG. 8.—Belt transect chart (scale 1 : 10) of the under-shrub and herbaceous vegetation of a mossy spruce wood in Norway. The figures represent decimetres. The left-hand column represents a belt about 2 centimetres wide, i.e. practically a line transect, and contains records of the five commonest species only, with a great preponderance of *Vaccinium vitis-idæa* (generally dominant) and *Aira* (*Deschampsia*) *flexuosa* (locally dominant). The rest of the chart represents a belt 5 decimetres wide, and contains records of the less common species only. (From Arrhenius.)

A scale large enough to prevent the overcrowding of symbols should always be chosen.

THE BELT TRANSECT (Figs 8 and 13) is a strip of vegetation of uniform breadth, for instance a decimetre, 6 inches, a foot, a metre, or even more. It is bounded by two parallel tapes, and the vegetation included between them is charted. For the trees of a wood a metre may be too narrow for the transect—5 metres may be necessary—for a very close uniform herbaceous vegetation of small plants a decimetre may be quite broad enough. The charting scales will be the same as those of the line transects.

The method of charting is the same as for a *quadrat* (see below). The belt transect chart to a certain degree combines the advantages of the line transect chart and the quadrat chart. While it is designed mainly to show the detailed changes of vegetation met with in passing along the line of the transect, the broader belt transects also give width enough to show the distribution of the individual plants in two dimensions.[1]

THE QUADRAT AND OTHER FORMS OF OBSERVATIONAL UNIT

A quadrat is simply a square patch of vegetation of any desired size enclosed within four tapes or laths for purposes of record. The simplest kind of record is a list of the species enclosed within the quadrat. To this may be added the number of individuals of each species. A large number of such list quadrats taken at random from, but well distributed over, a typical area of an association or consociation are necessary for determining its composition in quantitative terms. Numerical data obtained in this way can be dealt with statistically by modern methods and valuable quantitative information about the type of distribution of a species over the area of a community and the relations of different species to one another can thus be obtained. This is an aspect of ecology which is now being actively developed and is too specialised and technical to fall

[1] More detailed information about the methods of making transects is given in *Practical Field Ecology* by McLean and Cook, Chapter 6.

within the scope of the present work. It should, however, be noted that different forms of observational unit may be used. One of these is obtained by the use of a metal ring (say 1 foot in diameter) which is thrown down at random within the area of a community (over the shoulder if it is desired to eliminate completely any possible unconscious choice of location). The species occurring within the ring are then listed and the operation repeated for any desired number of times, say 50. In this way the species composition of the area is very thoroughly determined by the number of times each species has been found within the ring.

For charting purposes, however, for many reasons a figure with straight sides rather than a circle is preferable. The quadrat is the simplest and in some ways the most convenient, but it has been shown (A. R. Clapham, "The form of the observational unit in quantitative ecology," *Journal of Ecology*, **20**, 1932 and **171**) that oblongs in the form of relatively narrow strips give more information about a community than the same number of quadrats of identical area. This conclusion applies to charting as well as to the data gained by listing and counting which are intended for statistical analysis. The following description, which applies to quadrats in the strict sense (i.e. square areas) can be easily adapted for any other form of rectangle which it may be desired to employ.

THE QUADRAT CHART.—The standard size of a quadrat is taken as one square metre, and for herbaceous vegetation this is plotted on a scale of 1 : 10, i.e. on a square decimetre of millimetre paper such as is sold for drawing graphs. This can be conveniently mounted at one end of a card cut to 6 by 4½ inches (as shown in Fig. 9), such as are used for mounting the field sections of Ordnance maps (see p. 94). The margin of about a quarter of an inch on three sides of the actual chart is convenient for writing location, scale numbers, date, etc. Below the chart about 1¾ inches of card are available for the names of the plants, with the symbols used, and any

additional notes. These can, if necessary, be continued on the back of the card.

The boundaries of the quadrat are made with tapes or laths pegged with meat skewers or surveying "arrows" at the corners. The boundary tapes or laths should be marked in decimetres.

In charting close vegetation consisting of numbers of small

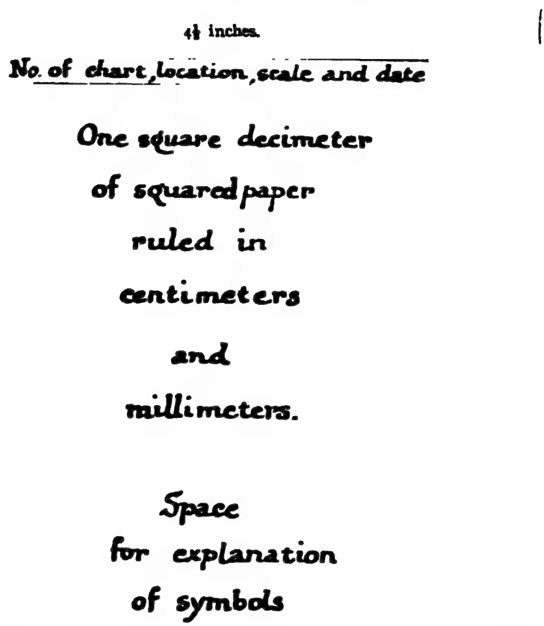


FIG. 9.—Diagram showing method of mounting blank quadrat chart on card. The diagram is one-half (linear) of the original.

plants it is well to have a wooden metre scale, and to lay this parallel with and one decimetre from the bottom boundary lath or tape, thus cutting off a strip a decimetre broad. A blank chart or a decimetre scale may then be laid a decimetre from the end of this strip so that a square decimetre of vegetation is enclosed. The charting of this square decimetre on the corresponding square centimetre of the chart is then proceeded with, and when finished the decimetre scale is moved a deci-

metre along the strip and so on, until the strip is completed, when the metre scale is moved another decimetre up, and so on until the whole quadrat is charted. In this way, i.e. by charting a square decimetre at a time, the maximum of ease and accuracy is obtained. In charting each square decimetre the "joins" with the adjacent ones already charted are checked with the symbols already made. By starting at the bottom and working upwards injury to the plants by lying on them before they are charted is avoided. These precautions are very necessary when working with dense vegetation to which the eyes must be brought very close. If the quadrat is to be photographed this should be done before the charting is begun, for the same reason.

For very close vegetation, consisting of a great number of individual plants in a small area, the scale of 1 : 10 is not sufficiently large. A scale of 1 : 5 is usually large enough for such communities, though in extreme cases 1 : 2, or even 1 : 1, may be necessary. The chart should be of the same size (one square decimetre), but each square centimetre of the chart will then represent respectively 25, 4, or 1 square cm. of the vegetation.

At the other extreme, quadrats of woody vegetation, for instance scrub or forest, must be much larger than one square metre. Quadrats of five or ten metres square are often large enough, though in a mature forest of large trees even the last-named size may not be sufficient, and the grid method is more suitable. It is seldom possible to include both trees and shrubs and also herbaceous ground vegetation in the same quadrat chart, because of the very different scales required.

The scale chosen for any quadrat should be such that each symbol occupies about the space corresponding to that covered by the plant represented, so that in a closed community the chart is well filled without being overcrowded, and in a partially open community the proportion of the total space covered by symbols to the total of the gaps is approximately the same as that on the ground.

FIG. 10.—Facsimile of a field chart of a permanent metre quadrat on standard scale (1 : 10), showing a stage of succession from bare gravel to heath association (*Calluna-Erica cinerea*). Note the large proportion of the surface covered by *Polytrichum piliferum* and *Agrostis canina*. Seedlings of *Calluna* and *Erica* are numerous and there are some larger plants of these species.

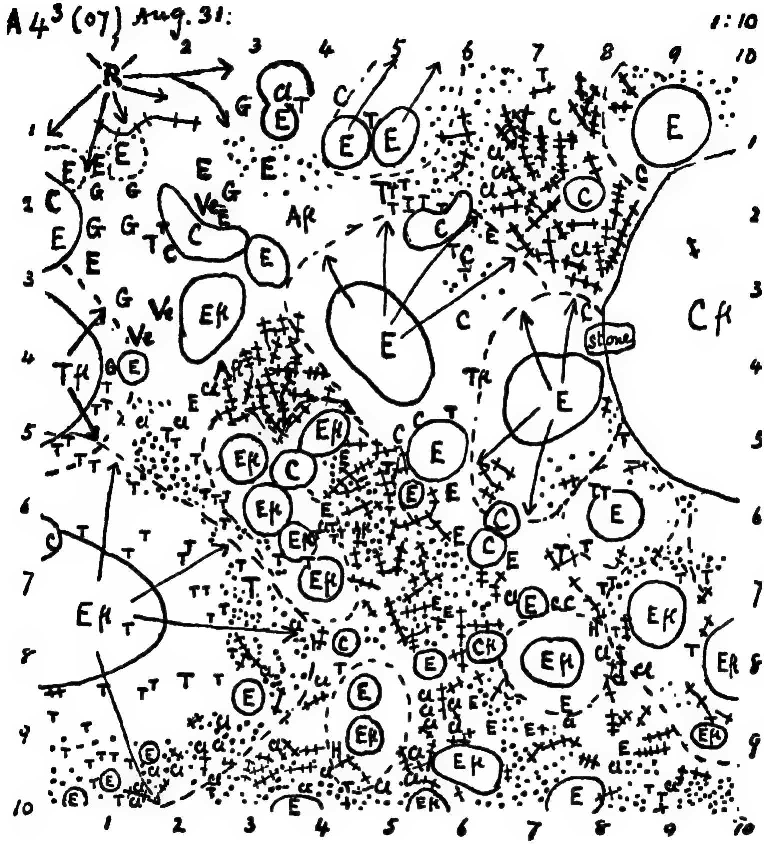


FIG. 11.—Facsimile of field chart of the same quadrat two years later. Note the rapid multiplication and extension of the two heaths (especially *Erica*), which now cover about half the area of the quadrat, and the corresponding restriction of *Polytrichum* and *Agrostis*. *Teucrium scorodonia* has also increased greatly, especially in the shelter of *Erica*. The few other species are subordinate. Symbols as in Fig. 11. The suffix *fl* means that the individual plant is in flower. The continuous lines indicate the outlines of the tufted plants, the interrupted lines the limits of the shade they cast. Probably a nearly continuous Ericetum with some *Calluna* is in process of formation. This is a frequent seral stage in the redevelopment of heath, preceding and ultimately giving way to Callunetum.

Tufted or cushion plants, covering a considerable area, should be outlined on the chart. The horizontal spread of the branches of plants casting considerable shade may be indicated by an interrupted line. Trailing branches may be indicated by continuous lines starting from the symbol (stock) and ending in an arrowhead. A distinct kind of vegetation, forming for instance a distinct stratum of the community, such as a moss or lichen stratum, may sometimes be indicated by a different type of symbol, for instance diagonal or horizontal lines, dots, crosses, etc. Figs. 10 and 11, which show the nature and rate of advance of heath plants during two years on an area which had been bared some years previously, will illustrate the use of these symbols.

It is not of course necessary for all purposes to chart a quadrat by the rather laborious method described, on millimetre squared paper and on a standard scale. Quadrats designed only to show certain features, for instance the number and distribution of the individuals of certain species, may often be charted in a few minutes accurately enough to serve the purpose, and may be of any convenient size and scale, though the scale actually used should always be ascertained and noted. For such purposes a notebook with paper ruled in tenth or quarter inch squares is convenient. It is for the accurate recording of the whole of the vegetation of typical samples of a community which is being studied, and especially for obtaining the data for detailed successional studies, that standard paper and scale and careful thorough charting are required.

For successional studies the quadrat must be made permanent, and this should be done by driving in flush with the ground-level at least two (preferably all four) corner pegs of metal or well-seasoned wood, and then measuring the distances or reading the angles made by lines drawn from the quadrat to at least two objects in the neighbourhood which are at once conspicuous and permanent. Careful and accurate notes of these data must be made.

PROFILE CHARTS

THE STRATUM TRANSECT.—This is a profile of vegetation, drawn to scale, and is primarily intended to show the relative heights of the plant shoots. It is based on the line transect, and is the complement of the belt transect (pp. 122–4). The line transect shows the distribution in one dimension, the belt and stratum transects in two, the profile or stratum transect including the vertical dimension. It is made by running the measuring tape along the line of the desired transect, and measuring with a wooden metre or foot rule, held vertically, the heights of the individual plants touching the tape. When the plants are tall it conduces to rapidity and accuracy of drawing, to fix one or more horizontal strings or cords, attached to vertical stakes at definite heights (according to the height of the vegetation) above the measuring tape. "Sag" must of course be avoided or allowed for.

The lateral spread of the individual plants at different heights should be indicated on the stratum transect chart. This is best done by a somewhat conventionalised representation of the plants of each species (Fig. 12, 13).

THE BISECT.—This name is given to a stratum transect chart which includes the root systems as well as the shoots (Figs. 12, 13, 14a). In making a bisect chart the shoot systems should first be plotted as described above. If it is possible a trench should then be carefully dug by the side of the transect line, to a depth greater than that of the deepest root system, the root system of each plant carefully isolated, and its vertical depth and lateral spread plotted to scale on squared paper. Great care has to be used to avoid breaking the finer ramifications of the roots.[1]

The work of making a detailed and accurate bisect chart is, of course, lengthy and laborious, especially where deep root systems are involved. It is often quite impossible to undertake,

[1] This thorough method was not adopted in making the drawings from which Figs. 12 and 13 were reproduced. Cf. Fig. 14.

if only because the digging of the necessary trench would not be allowed by the owner or occupier of the land. Nevertheless, the accurate recording of the distributions and mutual relations of root systems is of very great value. We are still largely ignorant of the facts of root structure and distribution in many of our commonest plant communities, and these facts are of

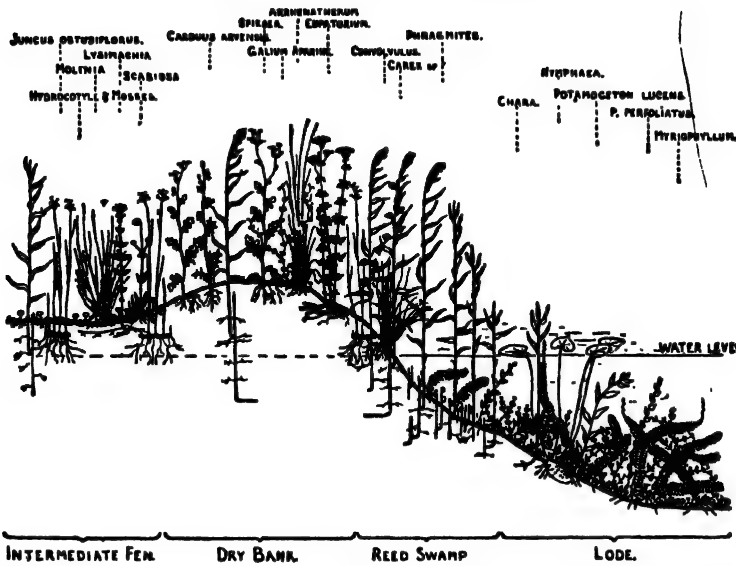


FIG. 12.—Bisect through edge of fen, bank and lode (drainage ditch) at Wicken Fen, Cambridgeshire. Scale, 1 : 60. (From R. H. Yapp.)

the first importance in any understanding of their economy. The very beautiful and instructive results obtained in America by Professor Weaver[1] (Fig. 14) fully demonstrate the interest and importance of the line of work. In spite of the obstacles and difficulties, the importance of this largely unexplored field must be pressed on the attention of students. Its intrinsic

[1] See, for instance, the figures in his *Ecological Relations of Roots*, and *Root Development in the Grassland Formation*. Carnegie Institution of Washington, 1919, 1920. Two of these are reproduced in Fig. 14, *a* and *b*.

interest and the knowledge that he is in two senses "breaking new ground," will amply repay the enthusiast who will face the trouble and labour of the undertaking.

It is not necessary to chart the root system of every plant on a long transect in order to obtain good results. The distribution and relations of the roots of a few individuals of differ-

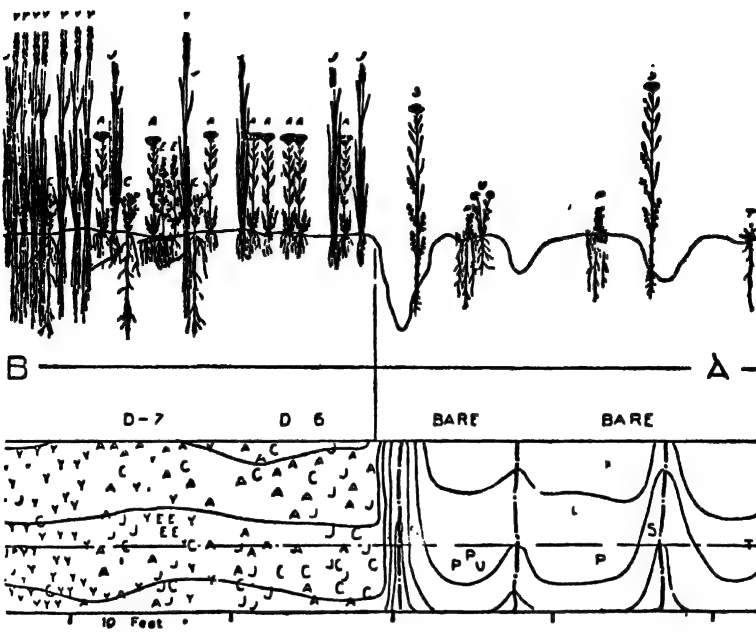


FIG. 13.—Belt transect and bisect charts in grassland used as cattle-range at 10,000 feet altitude on the Wasatch Mountains in Utah. On the left the slender wheat grass (Y) consociation is intact; on the right this vegetation is destroyed, the ground eroded as a result of heavy overgrazing, and occupied only by a weed community. Contour lines 1 foot apart vertically. (From Sampson.)

A, *Achillea lanulosa* (yarrow). C, *Chrysothamnus lanceolatus* (yellowbrush).
E, *Artemisia discolor* (sweet sage). J, *Stipa minor* (small porcupine grass).
P, *Pentstemon procerum* (blue foxglove). S, *Sophia incisa* (tansy mustard).
T, *Taraxacum* (dandelion). Y, *Agropyron tenerum* (slender wheat grass).

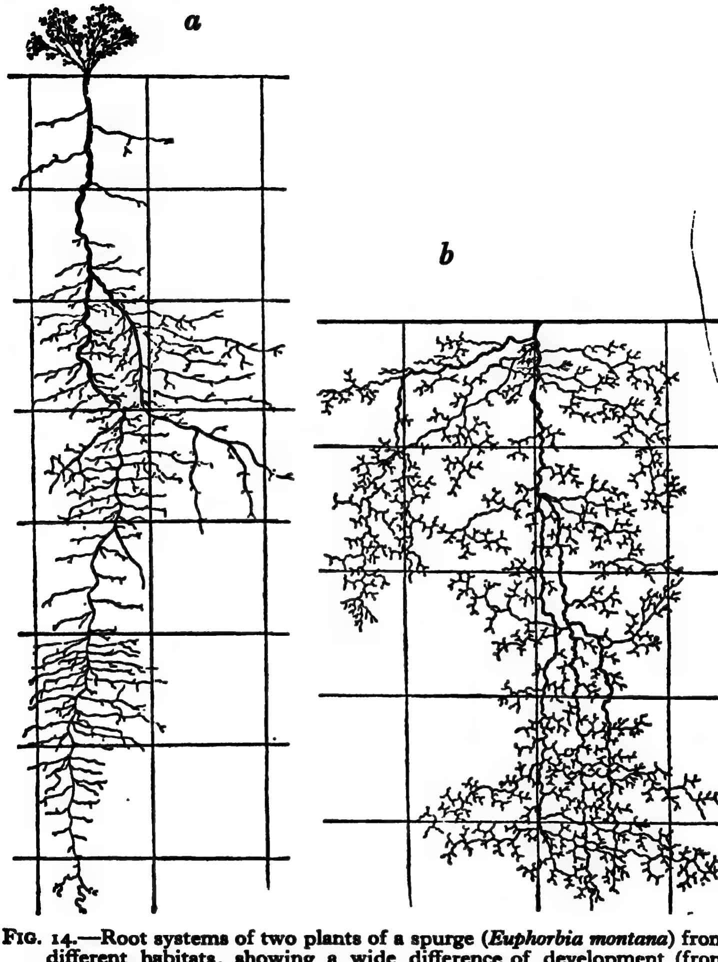


FIG. 14.—Root systems of two plants of a spurge (*Euphorbia montana*) from different habitats, showing a wide difference of development (from Weaver).

(*a*) Plant from the very compact dry soil of the Great Plains. The root penetrates more than 7 feet, with poor development of absorbing rootlets except in the third and fourth foot, where a fissure in the soil held water seeping from the surface, and in the sixth foot where the soil was moist and easily permeable.

(*b*) Plant from "gravel slide" on the Rocky Mountains. Here the soil is very coarse, loose and easily permeable. The rootlet system begins near the surface and extends only to the fifth foot, but the lateral spread is considerable. Each square represents one square foot.

ent species on chosen portions of the line will give much information, and similar useful work may be done in connexion with quadrat charts quite apart from a long bisect.

General Remarks on the Use of Vegetation Charts

Before leaving the subject of the charting of vegetation it will be well to insist once more on the objects of making charts. The general object is, of course, to obtain accurate records of the facts of structure of plant communities, just as the drawing of the external forms and internal structures of a species of plant is necessary to give us knowledge of the facts of specific structure. That plant communities have definite structures, constant within certain limits, is a fact of which anyone can satisfy himself by carefully examining any stable community. And a knowledge of this structure is essential for understanding the economy of the community, just as a knowledge of the structure of the individuals of a species is necessary to understand the economy of the species. We are therefore justified in aiming at accumulating accurate records of the one as of the other, and graphic records are the most accurate and instructive.

But just as the aimless drawing of casual sections under the microscope is of little value apart from the practice and experience the exercise gives, so the same thing is true of charting plant communities. In both cases the sample objects to be graphically represented must be chosen with a definite end in view if they are to be of the greatest value.

In the field of plant anatomy, if the general structure of a new kind of plant is not known, we want to have an accurate record of it, though the structure of some species is more interesting than that of others. And in the same way we want accurate records of the structure of all the well-defined plant communities we meet with in nature. This systematic recording by means of the appropriate charts is therefore a legitimate end in itself. It serves as a supplement to the general maps and descriptions of vegetation which are all that can be undertaken

in extensive work, just as microscopic anatomy serves as a supplement to descriptions and drawings of the external forms of plants.

But the communities of natural and semi-natural vegetation that we actually meet with differ from individual plants in that many of them are not stable organisms but transitory phases, which if left alone will develop into stable climaxes. To chart promiscuous samples of these *without knowing their status* is so much wasted time and labour. We get no sort of information that we can relate to anything else. As a matter of systematic record, then, our aim should be in the first instance to collect sample charts of the structure of the climax communities.

This sort of work, however, does not appeal to everyone, any more than does systematic plant anatomy. It is, in a certain sense, superficial work, because its end is systematic record rather than the opening of an avenue to the formulation of problems. And just as the plant anatomist may prefer to make a detailed study of the structure of a single species, and his interest may be centred in that structure as a working mechanism, so the interest of the student of vegetation may be centred in the intensive study of a single association or consociation with a view to learning how it came into existence and how it maintains itself. He will then not only record its adult structure, its variations, and the conditions under which it exists; he will also try to find out how that structure came to be built up, and its relationship to the communities which precede it in succession under different conditions. During such a study all kinds of problems will turn up, and their solution may be attempted by various methods. Among the methods which will have to be employed, charts will certainly be necessary, and selections from the most suitable of those described in this chapter may be made. For any thorough study of succession, as already noted, detailed quadrat or transect charting is essential, though certain successional problems relating to single species may be solved by less thorough methods.

Finally, a word may be said here about the great *educational*

value of quadrat and transect charting to the student because it leads the attention to the details of vegetation exactly as drawing a section under the microscope leads the attention to the details of tissue structure. No one can become an expert plant anatomist unless he has given the continuous attention to details of plant structure which is involved in learning how to draw and in constantly drawing microscopic sections; and no one can become an expert in the finer structures of vegetation unless he has given them the same kind of attention, which is involved in the effort to represent them graphically. In both cases there is the danger of falling into routine, of making the graphic record the end in itself; in both cases the mind should always be kept open to the problems raised by the detailed facts of structure observed, and efforts made to solve them.

CHAPTER XI

Intensive Studies—continued. Individual Species and the Parts They Play in Forming Communities

It was said in Chapter III (p. 28) that the study of a plant community always and necessarily drives us back to the individual species, and we begin to realise how little we know about them. One of the first things of which we realise our ignorance is the life history of the different species in the conditions under which they actually grow in nature. The fundamental importance of detailed autecological study cannot be overestimated.

Maintenance and Dispersal of Species.—Take, for instance, the herbaceous vegetation of a wood. What do we know of the actual means by which the different herbaceous species maintain themselves from year to year, or spread from one place to another? In the case of any given species, does it regularly ripen seed? and if so, how much? Different species vary enormously in the amount of seed they ripen and in the viability of their ripe seeds. It has been shown (Salisbury, *The Reproductive Capacity of Plants*, 1942) that on the whole a species produces more than enough seed to ensure survival and to have a chance of increasing its range when opportunity offers. Plants growing in shady places ripen fewer seeds, but these are on the whole larger and have a greater stock of reserve food, so that they are more likely to produce new plants that can establish themselves successfully. "The largest seed productions are characteristic of species associated with the habitats that are only intermittently available for colonisation, such as

woodland clearings and the intermittently exposed mud of shallow lakes and ponds" (Salisbury, 1942, p. 232).

Does the seed of a particular species fall and germinate on the spot, and do the seedlings establish themselves and grow into plants, which flower in their turn? Is seed spread to new areas, and does it thus increase the distribution of the species? All these questions require specific answers based on exact observation, for the process of reproduction by seed may be interrupted at any point in the series of processes.

The maintenance of perennial species—and nearly all woodland plants are perennials—is effected by the persistence of the original plants from year to year, or by the outgrowth of rooting offsets, or by some other means of vegetative reproduction. In addition to this, new plants may be produced, so far as there is room, by seed falling and germinating among the parent plants. On the other hand, dispersal from one place to another must take place by the actual carrying away of some part of the parent plant, and in the great majority of cases it is the seed which is so carried. Does such dispersal occur, and if so what are the carrying agents?

We are taught in the textbooks that many seeds or fruits have definite aids to dispersal; for instance, plumes or wings, which by offering a greater surface, and therefore increased resistance to the air, cause the seed or fruit to fall more slowly to the ground, and thus enable it to be carried further by the wind before it alights; hooks or some sticky substance which may attach the fruit or seed to some passing animal, by which it is carried to a distance; or a fleshy envelope which is eaten by a bird or quadruped, the seeds being afterwards voided. There is no doubt that species *are* dispersed in all these ways, but it is equally certain that the "dispersal mechanisms" are by no means always effective, that the seeds of plants possessing them are not always carried by the agents (wind or animals) that seem appropriate. We must also take into consideration the vast number of species that have no special "aids" to dispersal.

The questions we have to answer in studying the spread of vegetation are not concerned primarily with general categories of "dispersal mechanisms," but with the actual ways in which particular species are dispersed in particular places; and this is a problem—by no means always an easy one—which can only be solved by direct observation in the field.

It is clear that seeds or fruits which are carried to a distance from the parent plant do not all germinate, and if they do germinate the seedlings may not succeed in establishing themselves. The vast majority of viable seeds that do not find suitable soil in which to germinate are permanently lost. After a longer or a shorter time the embryo dies. We do not know where they go, because they are too small and inconspicuous to be traced. Sometimes large unmistakable seeds or fruits, such for instance as acorns or beechnuts, may be found lying on the ground in places where they are very unlikely ever to germinate, or, if they do germinate (owing, for instance, to continuous heavy rain), to survive. Young beech seedlings have been found in chalk grassland at some distance from the nearest parent trees, but on a dry soil so extremely shallow above solid chalk that the primary root soon dried up and establishment was impossible. And acorns in great masses are found in every good acorn year on ground where they have no chance to establish themselves.

The deathrate of seedlings, like that of all young organisms in a state of nature, is enormous. Both beech and oak seedlings, after good beechnut and acorn years, are found in immense numbers on the floors and on the edges of woods. But the vast majority disappear in the course of a few weeks or months. Some years ago a systematic effort was made to ascertain the causes of this, and with considerable success (**158** Watt, 1918, **159** 1923, Part I).

The sort of case we often meet with is the colonisation of a new suitable habitat by a species at some distance from the nearest parent plants, while unsuitable habitats at an equal distance remain uncolonised. The most obvious hypothesis to

explain this common occurrence is that seeds from the parent plants are spread everywhere, at least to that distance, but that all die except those which reach the suitable habitats. This may very often be true, but it is not necessarily always true. There may be some dispersal factor which takes seed only or mainly to the particular new habitat. For example, a new tree plantation on arable or grassland may receive seed from the woodland plants of neighbouring woods carried by woodland animals or birds, or on the clothes or boots of woodmen, beaters or sportsmen (**167** Woodruffe-Peacock, 1918). Sometimes what would appear equally suitable new habitats remain uncolonised. On the other hand, it is difficult to explain the constant appearance of the common ling (*Calluna*) in suitable new habitats, except by supposing that its seeds are very widely and generally dispersed by the wind or by birds, and that they germinate and establish seedlings only in suitable spots. But direct proof is as yet lacking.

A knowledge of the means of maintenance of a species in a place where it is already established can often be obtained by direct observation at different times of the year. Do the already established plants persist from year to year? Do any of them die, and if so, why? Does the species regularly or occasionally produce ripe seed, and do these seeds fall close to the parent plants, germinate, and produce new plants which successfully establish themselves? Sometimes all this information can be obtained by simple observation. A permanent quadrat, charted in succeeding years, will give accurate quantitative information as to the appearance of new plants from seed and the disappearance of the original ones.

One method of studying dispersal is by observing the appearance of new species where they did not exist before. In the first place, one has to be quite certain that the species was not present all the time, though so hidden or inconspicuous as to be missed. After a coppice is cut, for instance, many species which have been dormant or nearly so in the deep shade of the fully grown coppice, represented mainly or entirely by

rhizomes or other underground organs, burst into vigorous growth and flowering. Disturbance of an old soil may bring to the surface, so that they germinate, seeds which have been deeply buried and therefore dormant owing to deficiency of free oxygen, perhaps for many years. New plantations on old arable land or old grassland, and new habitats of all kinds, are particularly favourable for establishing the fact of migration from a distance.

The actual agents of carriage are often hard to determine. Much can be learned about wind carriage by observing the transport of winged and plumed seeds and fruits during gales of exceptional force. It is probable that occasional gales are very important in distribution. The distance to which winged and also small light seeds and fruits can be carried by the wind is still a matter of some controversy. It appears that aerial eddies may take small seeds and spores up to great heights where they can be carried by wind for very great distances before falling. Close observation of the habits and food plants of animals, both wild animals, especially birds, and also cattle, sheep, and horses, will often give a clue that may be successfully followed up. Man himself as a carrier of seeds is by no means to be neglected. But such observation is unlikely to be successful unless a keen taste for it exists in the observer, while long continued practice and unlimited patience are also essential. The study of animal carriage is in fact a special field which only a few born naturalists are well qualified or are likely to enter. Our existing knowledge of the whole subject is extremely fragmentary.

Short distance dispersal can be studied by observing the actual extension of a species from year to year. Favourable cases for investigation have to be looked for carefully: many species in many habitats are practically stationary. When a favourable instance has been discovered, the rate of advance can be measured by permanent quadrats or transects of suitable size on the edge of the area, and the means of dispersal can usually be ascertained in the course of the observations of

these. The advance of a perennial species is often effected almost entirely by the growth of rhizomes or runners.

COMPETITION AND THE ESTABLISHMENT OF NEW CONDITIONS. —In a community of perennial plants the number of fresh seedlings that can establish themselves among their parents is limited by the available space. This does not, of course, necessararily mean that the number of plants can increase till the shoots are in lateral contact. The root systems of plants growing spaced out from one another may occupy the whole intervening soil and thus use all the available water in the soil, so that though there is physically room for more *on the surface*, new individuals cannot establish themselves, though the seeds may germinate. Thus we get an *apparently open* community in stable equilibrium with its habitat. With a greater water supply, more individuals, of the same and of other species, are able to come in, till eventually we get a *closed* community in which the shoots are in lateral contact. The competition is then for space and light. If tall plants form part of the community, there will be room below them for lower growing plants, and thus we get the beginning of stratification. But these lower growing plants must be able to do with illumination less than full light from the open sky, for some of the light is cut off by the taller plants. When species of several different heights come in, the layering is increased, and in a temperate forest there are commonly four strata—trees, shrubs, herbs and mosses; though in forests (for instance tropical rain forests) very rich in woody species of different habits of growth there may be several more strata in the structure of the forest; and where the tree canopy is very dense, so much light is cut off that shrubs and sometimes even shade herbs are unable to grow and the vegetation consists of one or two strata only. As the number and variety of species and the bulk of vegetation increases, more humus accumulates in the soil, and thus alters the character of the soil, rendering it suitable for other kinds of plants.

In this way we get increasing differentiation, increasing complexity of the community, somewhat parallel with the differen-

tiation and increase in complexity of an advanced animal or human community, where also there exist different categories of members playing very different parts in the life of the community as a whole, but all dependent on the total food supply available.

Eventually, however, a limit is reached, determined partly by the number of species existing in the neighbourhood, and able to reach the community, and partly by the structure and economy of the community itself. For these exclude species unable to fit into that structure and economy when it is once well established, on account of the limitations of light and water supply, the constitution of the soil as modified by the existing plants, and other factors. The later stages of development of a climax community are often marked by an actual decrease in the number of species, since many of those that flourish in the middle stages of development, where the conditions are intermediate and very varied, are unable to subsist under the ultimate more extreme and more uniform conditions, for instance the deep shade of a wood in close canopy with its damp atmosphere and richly humous soil.

The processes which have gone to the making of such a complex community, given the power of arrival of the species which compose it and the general nature of the habitat, are two: competition and the establishment of conditions by some of the species which enable certain other species to exist. Generally speaking, the members of different layers do not compete, because their shoots and very often their roots occupy different strata. It is the business of the student of vegetation to study these processes and to trace out in detail exactly how they lead to the building up of the community (102 Watt, Part II). It is well to start with a preliminary attempt to understand, in a general way, the structure and economy of the climax, the adult community, just as in studying a species of organism it is well to start from the adult form. But we cannot fully understand the significance of all the features of an adult except in the light of a knowledge of its development. The

forces which go to the maintenance of the delicately adjusted equilibrium of a complex organism or a complex community cannot be estimated until we know how they come to be so adjusted, for they are largely masked by the adjustment itself. That is why the biologist insists on the importance of the study of development, and the ecologist on the study of succession—the development of vegetation.

It is impossible to give a detailed account of the methods to be employed in this study because they are so infinitely various. Charting of the various kinds described in the last chapter is essential for an accurate and detailed knowledge of the structure of the various stages, and the information obtained in this way often leads straight to a closer understanding of the processes involved in succession—competition and the establishment of new conditions. But observation of the facts of succession is constantly making us ask what precisely, in quantitative terms, are the modifications in conditions which lead to the disappearance of one species and the appearance of another, for it must be remembered that every change of conditions affecting the life of plants can be expressed ultimately in terms of chemistry and physics. In other words, we want to measure the change in habitat factors and to determine which are effective in changing the community. We can often guess at these changes, more or less plausibly, but the unravelling and strict proof of the effectiveness of the different factors involved is not an easy or a straightforward task. The habitat factors are considered in succeeding chapters, but for their complete elucidation long continued work, requiring special laboratory training, is necessary, and this is not within the range of the beginner. Some of these problems, indeed, the most advanced contemporary science is as yet unable to attack with success.

Meanwhile an immense amount can be learned, and much of it has not yet been learned, by a thorough study of the facts of succession, aided by quite simple and straightforward observations on habitat, and wherever possible by field experiment. The beginner need not therefore be in the least dis-

couraged because he has no special training in physical and chemical methods, and is unable to conduct difficult laboratory analyses. There is more than enough for him to do without troubling himself about such advanced work.

The possibilities of field experiment to determine crucial points are practically unlimited, and field experiments have not, in the past, been nearly enough used. Thus where there is a suspicion that water supply is crucial, small patches of ground can be artificially drained or watered (**56** Farrow, IV, 1917; **38** Jeffreys, III, 1917), and though this procedure does not in itself give quantitative results, it does give very valuable qualitative information on this question.

Root competition is sometimes of crucial importance. The shallow roots of the trees in a beechwood, for instance, may so drain the surface layers of soil that few herbaceous plants, or none, may be able to establish themselves. This point can be tested by making a quadrat between the trees and cutting off their surface roots by digging a narrow trench along its boundaries. This may enable herbaceous plants or undershrubs to establish themselves within the area of the quadrat (**18** Watt,).

The effective value of different intensities of light in excluding or admitting species can sometimes be tested by sowing seeds in variously shaded parts of a wood and noting their germination and subsequent growth. Some plants can produce seedlings, but cannot permanently establish themselves under certain degrees of illumination. Others can vigorously develop their vegetative organs, but cannot flower or ripen seed. If the plants flourish and set seed perfectly well, some factor other than light, such for instance as difficulty of dispersal, must be responsible for their absence where there is room and the habitat is otherwise suitable. Many woodland plants can, as we know from common observation, flourish quite well in the open, provided they have a sufficient water supply and the air does not become too dry during their growing season. It is impossible in the field to separate the drying effect from the illuminating effect of direct sunshine. In all such experiments it must be remembered

that the nature of the soil may play an important part. A given total water content which is adequate on one soil is quite inadequate on another, because less of the water is actually available for root absorption (see Chapter XIV).

The effects of animals can often be determined by preventing their access in various ways (**56** Farrow, II, 1916; **158** Watt, 1919, **159** Part I).

In this chapter we have done no more than touch upon some of the main problems raised in the intensive study of vegetation, but it is hoped that enough has been said to enable the student to realise the enormous and varied field which is open, and some of the ways in which the study may best be approached.

CHAPTER XII

Photography of Vegetation

It need hardly be said that photographs of plants or of vegetation are of no scientific value unless there is some definite purpose which they fulfil with at least some measure of success. A large proportion of the photographs taken, and even a number of those which get published, are of little or no value from any point of view, i.e. they are neither instructive nor beautiful. Many subjects are photographed under conditions which offer no prospect of success, and even when the conditions are relatively favourable the plate or film is often carelessly exposed. Students of vegetation who use photography should concentrate on the production of a few really good negatives, each with a carefully considered and definite aim.

There are two main scientific reasons for taking a photograph of vegetation: first the desire to make a picture of a characteristic sample of some definite type, secondly to make a record for the purpose of comparison with other records, for instance with a future photograph of the same spot, or with a quadrat chart.

Under the first head we have the snapshots of the student engaged in reconnaissance or primary survey. Good snaps of characteristic landscapes showing the kind of country and including one or more typical plant communities are interesting and useful, and the more successful negatives may be used to illustrate a published account. It is impossible to lay down hard and fast rules for the taking of these. Landscapes showing good contrast in bright diffused light are likely to be the best subjects. Though some subjects, especially distant ones, photo-

graph well in bright sunlight, this is generally to be avoided where the vegetation is at all close to the camera, because the excessive contrast and heavy shadows will probably obscure the forms of the plants. When a light stand is carried or the camera can be rested on a support, and the lens focussed on the screen, it is of course possible to make a time exposure and to obtain a greater depth of focus by stopping down the lens, including plants in the foreground. Focussing must then be carefully adjusted to get sharp definition of the objects nearest the camera, and a small stop used.

When time is available for the taking of more leisurely photographs with a larger stand camera the best possible negative should be aimed at. First of all the importance of good composition and satisfactory contrast may be emphasised. A good pictorial effect is by no means negligible from the scientific standpoint. A pleasing and effective picture impresses the features of a subject on the mind much more strongly than an ugly or poor one. The best weather and time of day to secure the best lighting should be carefully chosen.

A good orthochromatic (isochromatic) plate or film should be employed in photographing vegetation. The Wellington "anti-screen" plate is a suitable brand for ordinary use.

In making exposures it should always be remembered that vegetation usually shows some heavy shadows, and if the details in these are to be visible, sufficient exposure for this purpose must be given. Nothing is more unsatisfactory than photographs with the sharp range of tones giving a "soot and whitewash" effect, and this may be avoided by developing the plates in a solution which contains rather less than the normal amount of alkali. If the negative contains full detail, the desired result may be obtained by printing on bromide paper, by giving a full or abnormally long exposure and by developing with a diluted solution. In order to obtain negatives which are rich in detail pyro-metol is recommended as a developing agent.

Where a long exposure can be given, the Ilford or Wratten pan-chromatic plates may be employed with a light or colour

filter (one of the Wratten K series, or the special filter sold by the Ilford Company). In this way a much more correct rendering of the different tones of green occurring in vegetation is obtained. The colour of the filter must not be too deep, or the tones may be "over-corrected," so that the foliage appears abnormally light in the photograph. The plates or films must be developed in the dark (i.e. with the aid of a time-factor), or the plates may be stained before development with a desensitising solution of safranin.

Vegetation generally shows up best in a photograph if it is lighted laterally and not from above. For this reason photographs taken shortly after sunrise or shortly before sunset (with the sun behind or to one side of the camera) are often very satisfactory. The light, of course, must be yellow and not red. A little before sunset, also, the wind often drops and the air becomes calm, thus enabling a time exposure to be given. Wind is in general a great nuisance to the photographer of vegetation.

Portraits of individual plants should be most carefully focussed. They are often most satisfactory if the plant to be photographed is backed by a piece of material serving as a screen, against which the form of the plant shows up sharply. If taken against a background of vegetation the lines of the portrait are liable to be confused with those of the plants behind which are out of focus.

Stereoscopic photography is very valuable for the recognition of individual plants in a community, though the necessity of viewing them through a pair of lenses detracts considerably from their value as a means of illustrating a paper. The appearance of relief seen in stereoscopic photographs is a great help in recognising individual plants which would be scarcely separable in an ordinary photograph. Stereo-photographs are best taken with a stereoscopic camera, but they may also be obtained by making two successive exposures with an ordinary camera which has its optical axis moved laterally by 2–3 inches between the two exposures. By the latter method exaggerated relief may be obtained, or fairly distant objects such as the trees in a wood

may be made to stand out better than they would in photographs taken with an ordinary stereoscopic camera, the amount of relief depending on the distance through which the optical axis of the lens is moved.

In photographs which are simply scientific records it is rarely possible to consider pictorial effect, and even a poor negative may be better than none at all, though naturally the best negative possible under the circumstances should be aimed at. In this category come photographs of quadrats, transects or areas which are being mapped. The quadrat boundary laths, transect tapes, etc., should always be included. They give a certain definiteness to the photograph which is useful and effective.

In photographing a quadrat the camera is best placed a little outside the bottom boundary, tilted forward so as just to include the length of the front lath, focussed on the middle of the quadrat and stopped right down. The quadrat will appear as a trapezium, but the vegetation will be less foreshortened than if the camera is horizontal. When the whole of the vegetation included in the quadrat is very low, forming a carpet with no plants rising much above the general level (e.g. a turf or moss community), it is a good plan also to photograph the quadrat, or part of it, with the camera pointing vertically downwards. This can be managed with the help of a ball and socket "universal joint" screwing to the top of the stand.

Permanent quadrats, especially of communities with well-marked aspects, such as woodland ground vegetation, meadow land, etc., should be photographed in each aspect, i.e. several times in the season. At the least all permanent quadrats laid down for the purpose of studying succession must be photographed once a year—if possible when the vegetation is at its maximum luxuriance, and always at the same date, or at least within a few days of the original date.

Photographic records of vegetation which are intended for comparison with others of the same spot taken at earlier or later periods should be photographed with the same camera in *precisely* the same spot at *precisely* the same height and

pointing in *precisely* the same direction. Even a slight deviation in any of these respects will render *exact* comparison impossible. The best way to secure this result is to drive a permanent peg into the ground exactly under the middle of the camera, and a taller stake so that it comes exactly in the middle of the picture, and can be focussed upon. If a note is made of the height of the lens above the ground, succeeding photographs which are strictly comparable can then be taken (see **173** Farrow, 1925).

Photography of vegetation from the air has in recent years produced remarkable results. Not only does it provide a rapid and accurate method of recording the distribution of different types of vegetation, but species of dominant plants can often be identified in photographs taken from a height of several thousand feet. It is expected that such photographs covering the whole country will be made available in the not remote future, and they will be of great assistance to students of vegetation. Air photographs have to be carefully correlated, of course, with observations made on the ground.

PART IV

The Habitat

CHAPTER XIII

The Habitat. Climatic and Physiographic Factors

IN modern ecological work the term *habitat* may be taken to mean "the sum of the effective conditions under which the plant or the community lives." Originally it meant the *place* in which it lives,[1] but while the word is still commonly, and of course quite legitimately, used in this sense, it has now become a scientific term applied to all the conditions affecting the plant incidental to the place in which it lives. Thus we have to distinguish the general habitat of a community from the particular habitat of an individual plant belonging to it, for it is at once obvious that the conditions under which an oak tree lives are different from those of the moss growing upon its bark, though they have some points in common, for instance the general climate of the locality. (Cf. 168 Yapp, 1922.)

Every species and every community has a certain *range* of habitat, which may be wide or narrow. Thus some species are distributed over a large portion of the globe under a consider-

[1] From the Latin *habitat*, "it lives in" or "inhabits," e.g. *Primula habitat in silvis*, the primrose lives in woods: hence the habitat of the primrose is woodland.

able variety of climates, others are confined to a very restricted set of conditions, which may be realised only within a small area. It by no means follows that such a species *can* only live within the area to which it is actually confined. It may not have completed its natural migrations, and may still be in course of extending its range. All species *tend* constantly to increase their range, and it has been shown that the areas covered by species vary *on the whole* with their *age*, i.e. with the time during which they have been in existence.

But this tendency is by no means always realised. A species may be prevented by various kinds of barriers—oceans, mountain ranges, deserts, etc., or closed plant communities which it cannot enter—from spreading from the place to which it is in fact restricted, though if it is transported across these barriers to a suitable spot it will establish and propagate itself. This is well seen when European plants, especially "weeds," which have great powers of dispersal,[1] are transported to temperate North America or to New Zealand, or when plants from the Old World tropics are carried to those of the New World, and *vice versa*. Thus we may distinguish *actual* from *potential* habitats.

The same is true of communities, though in a much more restricted way, for a whole community has not the mobility which may be possessed by the single species.

Theoretically, of course, we should be able to analyse the different factors of the habitat into the ultimate physico-chemical forces acting upon the different organs and cells of the plant, but we are as yet far from being able to do anything of the kind: neither plant physiology nor physical chemistry is sufficiently advanced. Even the most highly trained student

[1] Due to a variety of causes. They commonly grow quickly and produce a large amount of seed in a short time; frequently the structure of their seeds makes them easily carried long distances by the wind. They may be unwittingly carried by man with crop seed or otherwise. They are generally "tough" or "hardy" plants and able to establish themselves and flourish on a wide variety of open soils. Thus, if a stretch of land in virgin country is ploughed, weeds will appear, though they could not cross the space separating the newly ploughed land from their nearest habitat without the aid of man.

of habitat factors has at present to be content with comparatively rough statements about the evaporating power of the air, the range of temperature and of soil water content, percentages of various mineral salts, hydrogen-ion concentration, and so on; and he is still far from understanding the different interactions of the various factors, or their exact effects upon plants of different structure and different types of metabolism. All this is of course outside the range of the beginner.

Much of the detailed exact study of the habitat factors is considerably more difficult than equally detailed exact study of the structure and distribution of vegetation. It is partly for this reason, and partly because the study of the latter is greatly neglected, that special emphasis has, in this book, been given to the vegetation itself. At the same time the student must recognise that he cannot understand vegetation adequately unless he acquires some knowledge of the habitat. Here we confine ourselves to the simpler and easier methods of approach to habitat problems. The keen student will gradually acquire a knowledge of the problems that he cannot solve by the simpler methods, and if time and opportunity are available will learn the techniques necessary to attack them.

For general purposes we may group habitat factors (ecological factors) into *climatic*, *physiographic*, *edaphic and biotic*, though the factors in the different classes are not always sharply separated.

Climatic factors include the general features of regional climate and season, light, temperature of the air, rainfall, humidity of the air, winds; but they may also vary locally (local climate) and even in extremely restricted areas (microclimate).

Physiographic factors are those determined by the general nature of the geological strata, by topographical features, such as altitude, slope, exposure, and by geodynamic processes like erosion, silting, the blowing of sand, and the like.

Edaphic factors are those dependent on the soil as such, its physical and chemical constitution, water content, aeration, etc.

Biotic factors are those due to living organisms, either animals or plants.

It will easily be seen that the factors assigned to different classes act and may react upon one another. Thus the climatic and physiographic factors influence one another, and both affect the edaphic and biotic, so that some of these last are largely due to the others. The factors classed as climatic have a dominating influence upon all the others.

Rainfall, the lithological nature of the strata ("rocks" in the wide geological sense), and their varying altitude, together determine the size and course of the rivers and streams, and thus the conformation, slope and exposure of the land. Altitude, slope and exposure determine what is called "local climate," affecting the temperature, rainfall, air moisture and insolation (incidence of radiant energy from the sun) to which a given piece of vegetation is exposed, and therefore to a large extent the particular species of plants that form it. Marked *local climates* exist on summit ridges, on steep northern or southern slopes, in deep ravines which are relatively cool and damp, and in shallow basins into which cold air drains and in which it lies during calm weather. Very limited cases of local climate are seen in the conditions obtaining on the leeside of a rock, or even a large stone, which may protect the immediately neighbouring plants from insolation and from wind, thus creating a *microclimate*. Similar conditions apply of course to the sheltered side of a wood and to the lower strata of woodland vegetation. Further, physiography and climate between them, together with the physical and chemical characters of the rocks, determine the nature of the soils that are formed, and thus the edaphic factors of the habitat.

The direct effect of edaphic factors is very great, since the root systems of land plants normally inhabit the soil. Both the physical texture and the chemical properties of different soils are important in differentiating vegetation, especially when they are extreme and work in the same general direction as the climatic factors (see p. 211).

The biotic factors of the habitat are due to the organisms which directly affect vegetation. Animals act upon plants in various ways, very largely by eating them or parts of them, but also by carrying pollen and seed, and by manuring and otherwise altering the soil.

Plants themselves, as we have seen in earlier chapters, profoundly affect one another, and the effects which they bring about are sometimes included in the biotic factors of the habitat. This use of the term is correct enough when we are considering the habitats of single species, but not of course when we are dealing with a plant community as a whole (see p. 153). Invaders from another community may, however, so change the habitat of the community as eventually to destroy it.

Community habitats change like the vegetation itself. Apart from effects due to the slow secular changes of climate and of physiography, the soil may be constantly changing by erosion, rain-wash, or silting, and in stationary soils by leaching (the washing out of soluble salts). These are all *allogenic factors* (see p. 46). The accumulation of humus, one of the most important of soil changes, is a direct reaction of the plant community itself upon its habitat (*autogenic factor*).

Thus we see that the habitat is a very complex thing, the result of the interactions of a host of different and varying factors. But we must always remember that their actual effect upon the plants (apart from the grosser direct effects of animals and of physical agents like wind, snow, rushing water, etc.) is resolvable into a few physical and chemical processes—the effect of light on photosynthesis and growth, the effect of temperature on the chemical changes in the plant body, the evaporating power of the air on the water in the plant, the effect of the soil solution and its contained ions on the root hairs and through them on the other tissues of the plant.

Climatic Factors

1. Light.—No reasonably easy and completely satisfactory method of determining the light intensities in different habitats,

and especially the *different* light intensities and qualities affecting the functions of plants, has yet been devised. Accurate measures of "total light" in absolute units can only be obtained with the "photoelectric cell," and the use of this is too expensive and difficult for the beginner. There are other difficulties in the way of measuring the light as it actually affects green plants. One of these is that light is essential to the life of green plants in more than one way. It provides the energy for photosynthesis, and it affects growth, probably in different ways; it also has a specific effect in the promotion of flowering. The particular rays of the spectrum which are most effective in these diverse functions are different. The ordinary methods of measuring light depend on its effect on chemical reactions ("photochemical effect") and the rays which are most active in these are not the same as those most active in photosynthesis. Though the chemically active rays (blue end of the spectrum) are on the whole those which affect growth and flowering (as distinct from photosynthesis), we do not know that their intensity, as measured by any chemical change which is convenient for record outside the plant, is exactly proportional to the intensity of the light effects upon the plant.

Nevertheless, measures of the rapidity of darkening of sensitive photographic paper are certainly useful for rough measures of the "light" of a woodland habitat at any given moment. It has been shown that there is considerable constancy in the depth of shade, as measured in this way, that a given species of herbaceous woodland plant will tolerate.

An ordinary actinometer such as is used by photographers —for instance the Watkins "Bee meter"—is the simplest instrument to employ. The time in seconds that a strip of the sensitive paper freshly exposed in the habitat takes to darken so as to match the standard tint, is compared with the time in the open. Since the time taken in darkening is inversely proportional to the light intensity, the light in the shaded habitat may be represented as a fraction of the light in the open by using the number of seconds occupied in the former in darkening to the standard

tint as the denominator, and the number occupied in the latter as the numerator. Thus, if the time occupied in the former is one minute and in the latter two seconds, the light in the habitat is $\frac{2}{60} = \frac{1}{30}$ of that in the open. The readings in the first instance should be made in bright sunlight near midday, the actinometer being held horizontally in the open, and perpendicular to the source of greatest illumination in the shaded habitat. In the middle of a close wood this will also be horizontal, since the greatest illumination is vertical. To neutralise inequalities of illumination which may occur under a canopy of varying density the actinometer may be moved slowly backwards and forwards during exposure over a typical patch of vegetation. The average of several readings will tend to reduce accidental errors. Besides the readings in bright sunlight it is well to take some in cloudy and overcast weather.

Sensitised paper stained with the pigment known as Rhodamin B can be used in the actinometer instead of ordinary photographic paper. It is specially sensitive to yellow light, which is important in photosynthesis. For details as to the preparation and use of Rhodamin B paper, see McLean and Cook, *Practical Field Ecology*, p. 142.

The minimum light intensity necessary to the existence of certain species or communities of the ground vegetation of woodland may often be determined by this method, at least for any given type of woodland. If great discrepancies are found between the apparent minimum illumination in different places other factors must be looked for, e.g. incomplete migration, competition of other plants, difference of soil moisture, variation of humus, etc.

It must be remembered that many woodland plants produce their leaves and flowers in the "prevernal aspect" (see p. 41), i.e. when a much larger fraction of the total daylight reaches the floor of the wood than is the case when the foliage of the trees and shrubs has developed. Readings should therefore be made during this "light phase," as it has been called, say in mid-April, as well as in the "shade phase" at midsummer

The light of the light phase is certainly very important to the prevernal species, and the subsequent shading affects different species in different ways, the leaves of some dying off in the shade phase, while those of others persist throughout the summer.

One drawback of the photographic actinometer method of light determination is that it gives records only at the moments at which readings are made. No really satisfactory method of integrating the total light received over a period of hours or days has yet been devised.

2. Temperature of the Air.—Single temperature readings are not of much use, save on exceptional occasions, but if an automatic thermograph, recording the temperature curve on a drum,[1] is available and can be safely set up in the habitat without risk of interference, useful results may be obtained, particularly as giving information on the range of temperature near the critical limits within which particular species exist. If in the open the thermograph must be protected from the direct rays of the sun. Sun temperatures cannot be recorded by the instrument.

3. Rainfall.—Indirectly this is a factor of prime significance for plants, but it is seldom a *direct* factor of importance. The total rainfall, and especially the distribution of rainfall through the year, is one of the leading features of climate, but sufficiently close figures can usually be obtained from the nearest rainfall station.[2] Where there is strong land relief, however (notably in mountain regions), the local rainfall often varies very considerably within quite short distances, and additional rainfall records in such places are very useful for meteorological as well as ecological purposes. An automatic rain-gauge is the most useful instrument. This registers the rainfall on a drum and empties itself automatically when the receiver is full, the pen

[1] These instruments require a new blank chart to be affixed once a week.

[2] The Meteorological Office (Air Ministry) has a number of trustworthy observers scattered throughout the country, who will always courteously respond to a request for local information. Through the Office any working ecologist can get into touch with local rainfall observers.

returning to the base line. Like the automatic thermograph, it requires a new chart once a week, and must be exempt from mischievous interference. For meteorological purposes certain precautions as to location of the gauge have to be observed, in order to correct deviation due to local conditions; but some of these do not apply to the measurement of rainfall in a given habitat, where local conditions are the important phenomenon which it is desired to record.

4. Humidity and Evaporating Power of the Air.—This is a very important direct factor, far more so than rainfall, since it directly affects the function of transpiration (loss of water by evaporation from the aerial parts of the plant), one of the leading functions through which the habitat of a plant is determined.

The commonest meteorological instrument for measuring *relative humidity* (the percentage amount of water vapour actually held by the air at a given temperature, the amount required for saturation at that temperature being taken as 100) is a pair of thermometers, one with a "wet," the other with a "dry" bulb. The "wet" bulb is surrounded with a gauze envelope connected with a little reservoir of water by a stout strand of cotton fibres, which by capillarity keeps the envelope of the bulb wet as evaporation proceeds. The jacket of evaporating water lowers the temperature of the wet bulb proportionally to the rate of evaporation, so that the difference between the temperatures recorded by the two thermometers is a measure of the deficit of water vapour in the air below saturation point at the given temperature. If the two thermometers show the same temperature, the air is saturated, and the drier the air the greater the difference of temperature they record. Hygrometrical tables show the relative humidities corresponding with given readings of the wet bulb at given dry bulb temperatures.

Wet and dry bulb thermometers thus record the relative humidity of the air at a given spot at a given moment, but they do not directly record the actual evaporating power of the air, which exerts the "pull" on the water in a plant, since this is higher

the higher the temperature, though the relative humidity may be the same. This "pull" is measured by what is called the *saturation deficit*, which is defined as the amount by which the partial pressure of water vapour in the air (usually measured in "millibars"[1]) falls short of the partial pressure at saturation point, whatever the temperature. Saturation deficit can be directly calculated from the difference between the readings of wet and dry bulb thermometers, since the temperature is known.

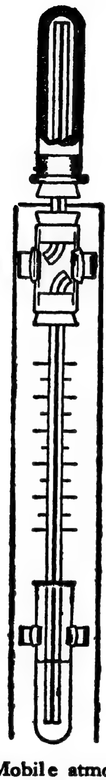
Wet and dry bulb thermometers can of course measure relative humidity and saturation deficit only at a given moment. A more directly useful instrument to the ecologist is the *atmometer* (*evaporimeter*), which measures the total evaporating power of the air at a given spot over any desired period, thus integrating the water vapour content of the air with temperature, wind and the time factor. Unless the air is completely saturated with water vapour wind raises the evaporating power of the air by constantly removing the saturated air in contact with a wet surface and replacing it by drier air.

Convenient forms of atmometer are shown in Figs. 15A and B. These were designed by Dr. W. O. James of the Department of Botany, Oxford, who has used 15A constantly both in the laboratory and in the field, and who very kindly supplied the drawings from which the figures have been reproduced.

At the top of Fig. 15A is an inverted "candle" of porous unglazed earthenware (shown in section above), the thick wall of which is represented by dotting. The mouth of the "candle" is closed by a perforated rubber stopper through which passes a thick-walled tube of millimetre bore open at the upper end near the top of the cavity of the candle. The lower end of this tube passes through the bored upper stopper of the *bubble trap* which is a piece of wide glass tubing closed at each end by perforated rubber stoppers. Another piece of thick-walled millimetre tube passes through the lower stopper of the bubble

[1] A millibar is one thousandth of the mean barometric pressure at sea level, and is the standard unit of pressure in meteorology.

trap and its lower open end dips into an open test-tube which



15A.—Mobile atmometer for determining relative rates of water loss under different conditions.

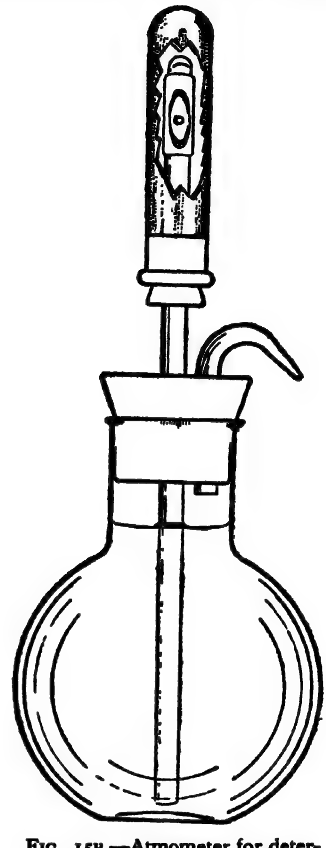


FIG. 15B.—Atmometer for determining weight of water lost over considerable periods.

is used as a *water reservoir*. The free ends of the two millimetre tubes within the bubble trap are bent in different directions.

Bubble trap and water reservoir are held by spring clips screwed into a stake which supports the apparatus, and behind the length of millimetre tube between the two is fixed a *scale* with arbitrary divisions.

The candle, bubble trap and millimetre tubes are carefully filled with distilled water,[1] care being taken not to admit bubbles of air, and distilled water is also poured into the reservoir into which the lower tube dips. As the water soaks through the porous surface of the candle it begins to evaporate from the free surface and more is drawn up through the tube from the reservoir. By admitting a bubble of air into the lower end of the lower tube and timing its passage over the divisions of the scale the relative rates of ascent of water in the tube, and therefore of evaporation from the candle under different conditions can be determined.

This apparatus can be placed in different positions in vegetation, as the stake can be of any desired length and can be moved at will. But it is designed for rapid readings and owing to its small reservoir it cannot be left for long periods.

The evaporimeter shown in Fig. 15B has a much larger reservoir enabling evaporation to be measured by the actual weight of water lost over longer periods. But owing to the size of the reservoir and the need for a balance it is not so easily manipulated as the instrument shown in Fig. 15A. It consists of a porous pot or "candle" and a wide-necked flask or bottle of 250 millilitre capacity. These are connected by a length of glass tubing reaching from near the top of the porous candle to the bottom of the flask. The glass tubing is sealed at the upper end and a small hole is blown in the side about an inch from the top. This is covered by a 1 in. length of springy rubber tubing which must be a tight fit on the glass. When the apparatus is set up this acts as a Schrader valve, allowing water

[1] Any impurity in the water tends to fill up the pores of the earthenware and thus to lower the evaporating power of the candle. Water containing lime does this very quickly. Rinsing with weak corrosive sublimate will keep the porous surface, which should never be handled, free from algal growths. The surface may also be cleaned occasionally with a stiff toothbrush and distilled water.

to be drawn into the candle, but preventing it from working back when the candle is saturated by rain. The candle, including the interstices of its walls, must be filled with water, without the inclusion of air-bubbles, and this is conveniently done by exhausting the air under water and returning the pressure two or three times. The tube is then filled with water, fixed into the candle with a rubber cork, and attached to the flask, which should be filled with water to the neck. The rate of evaporation is obtained by successive weighings. If the apparatus is made approximately to one and one-third times the size of the figure, convenient losses of weight will be recorded under conditions favouring rapid evaporation in periods of three or four hours, and the supply of water in the flask will be sufficient to last about a week. In the drawing, the candle and the rubber tubing are cut away in front to show the internal arrangement of the valve.

5. Wind.—Violent winds often break off twigs or branches of plants, especially of trees and shrubs, and in very windy situations the tree or shrub may be altogether prevented in this way from growing above a certain height; but the most important general effect of wind is to increase transpiration, by constantly bringing unsaturated air into contact with leaves and young shoots of plants. When a tree such as an oak is exposed to constant and violent winds, mainly from one general direction, not only does the trunk slope away from the wind but new shoots on the windward side are constantly dried and killed off in this way, so that the whole crown of the tree takes the form of an almost horizontal brush directed away from the wind. The same effect is seen in severely wind-cut scrub on exposed coasts and at high altitudes. The drier the air and the higher the velocity of the wind the greater is this effect. In its extreme form it can be seen by the "blighting" effect of a strong dry wind on the young shoots of all kinds of plants, especially of an east or north-east wind (the quarters from which the driest winds usually come in this country) in the spring. Under such conditions the whole of the young leaves

and shoots in exposed situations may be killed in a few hours, owing to the loss of water by evaporation being too rapid to be replaced quickly enough from the roots of the plants.

Even under less extreme conditions constant exposure to wind, commonly to the prevailing west and south-west winds, though these are more or less laden with moisture, may be of the first importance in determining the local distribution of species or communities. Certain trees are well known to the forester to be "wind-resistant," either because they are better protected against over-transpiration, or because their twigs and branches are less brittle. Thus beech is much more wind-resistant than ash or oak, and the latter cannot establish themselves on the exposed south-west sides of woods, while the beech can. In this way the succession of establishment of trees in forest development may be greatly modified locally.

Owing to decreasing friction with the soil surface the velocity of the wind increases very rapidly with increased height above the ground, and the effect of this on vegetation is often exceedingly striking. If a strong wind carries sand particles, these add an erosive effect to the drying effect of the wind itself, the sand being driven against the exposed parts of plants, pitting them, and, if the action is long continued, eventually disintegrating them. Wind-driven frozen snow particles have a similar effect, as may be seen on high mountains near the altitudinal limits of tree vegetation. These last mentioned effects are greatest at a certain small height from the ground, for below this height friction with the ground surface diminishes the velocity of the wind so that it cannot carry the particles, and above a certain height but few of the wind-driven particles can rise.

The velocity of wind is measured by special instruments (anemometers) at meteorological stations of the first rank, and there is a conveniently small portable instrument formerly made in Germany which could be used by ecologists for measuring the velocity of local winds. But in view of the fact that this is probably not now obtainable and that the evaporating effect of wind is integrated with other factors by the atmometer cup,

the student may be content with noting the direction and roughly the strength of prevalent or occasional winds.[1] The main thing is that his eyes should be open to the importance of wind, which is sometimes ignored or minimised.

Physiographic Factors

It has already been mentioned that strong topographical relief (steep hills and deep valleys) has a profound effect on vegetation, very largely because it produces characteristic "local climates" (see p. 156). This effect is more marked in less equable regions than Great Britain, whose climate is on the whole rather uniform.

Thus, to take one striking example from Southern Europe, the limestone ridge of Sainte Baume, in Provence, which runs east and west, bears on the north and south faces of its central portion totally different vegetations which have not a single species in common. The lower part of the steep northern face, on which fog often forms and which is entirely protected from the midday strength of the Mediterranean sun, bears virgin beech forest, with holly, yew, abundant lichens and a hygrophilous[2] ground vegetation. The south face is occupied by the highly xerophilous[3] Mediterranean "garigue" vegetation of sparse shrubs and herbs, whose leaves are strongly protected against evaporation. This complete contrast is entirely due to the difference of the local climates separated only by three or four hundred feet of precipitous rock face rising above the beech forest.

Similar differences, though seldom so extreme, are seen

[1] The "Beaufort scale," used by meteorologists to express the varying strength of wind, has 13 degrees from dead calm (0) to hurricane (12). With a little practice the different degrees can be estimated subjectively. Thus a gentle breeze (3) just keeps leaves and small twigs in constant motion (6 miles an hour), a gale (8) breaks off twigs of trees and impedes walking (30 miles an hour).

[2] Greek ὑγρός (hugros), moist, and φίλος, loved.

[3] Greek ξερός (xeros), dry.

everywhere except in the most arid and in the wettest regional climates. In the northern hemisphere, northern slopes usually bear a vegetation adjusted to damper conditions than southern slopes, and often the same communities as are borne by the southern slopes at a higher altitude. Generally speaking, the greater the altitude the damper the climate, except where there is a coastal fog belt so that the higher altitudes are drier. In Great Britain such differences are not, on the whole, extreme; but the vegetation, particularly the subordinate vegetation, of a deep sheltered ravine differs considerably from that of a neighbouring exposed slope. On the other hand, when a valley runs in the direction of the prevailing wind it often acts as a funnel and the vegetation of its floor may show the effects of wind more severely than the adjoining slopes. The effect of shelter on windy coasts and mountains is very pronounced. It has also been shown, as we have seen (p. 156), that local climate may vary considerably within a few feet or even inches on very uneven ground (microclimate); the shelter of a small rock or hillock sometimes making a difference, for instance to wind effect, that enables a plant or small community to grow which cannot exist outside the sheltered area.

Steepness of slope, especially in comparatively high latitudes, increases the effect of aspect or exposure. Thus in the northern hemisphere a steep southern slope will receive the rays of the midday sun almost or quite perpendicularly, while a steep northern slope may receive only oblique rays in the morning and evening, or none at all except perhaps for a short period at midsummer, and this difference of insolation sometimes affects the vegetation quite markedly. A simple home-made clinometer is a useful instrument for measuring the angle of slope in a hilly country, and with compass bearings the maximum possible time of direct illumination can be calculated, if desired, with the aid of the necessary astronomical data.

The nature of the underlying rock is often reckoned as an edaphic factor, and so it may be; but in so far as it determines topography it is physiographic. Different types of crystalline

rocks, hard and soft limestones and sandstones, stratified shales and unstratified clays, alluvium of different kinds, will produce different topographies, and thus, in conjunction with the climate, affect the physiographic factors. A discussion of such matters belongs to physical (dynamic) geology, some knowledge of which (and the more the better) is necessary to the ecologist in most areas.

In areas of relatively mature land structure, such as we have in the Midlands and the south and east of England, the topography is changing very slowly. The land forms are relatively static, and geodynamic changes are not now altering the conditions of vegetation except locally and on a small scale.

It is otherwise in mountain districts and on the sea coast, where geodynamic agents are active. Here the topography may be constantly shifting, destroying the habitats of some communities and creating new habitats. Rock faces, cliffs, steep slopes, and river banks that are being eroded present a special class of habitat in which certain species maintain a precarious existence. If the erosion is rapid enough no species may be able to secure a foothold. Streams cut back into plateaux, increasing the drainage and diminishing the water content of the soil. The eroded material, gravel, sand or clay, or a mixture of these, is brought down by the stream and deposited as silt along its lower course, or creates a delta where the stream flows into a lake, thus providing new habitats for vegetation of different types. Frost, again, breaks up the rocks on flat exposed mountain tops, producing the special type of habitat consisting of more or less loose rocks of various sizes, known to the geologist as "mountain-top detritus." Frost and water between them cause the fall of rock fragments from a rock cliff and thus produce screes at its foot—another type of habitat. All these processes change old habitats or create new ones, and present innumerable problems to the ecologist, both successional problems and problems relating to the factors actually at work in determining the vegetation which appears. The geodynamic factors may, as in the case of an evenly eroding rock face,

actually maintain a constant type of habitat, and thus a constant type of vegetation, though the individual plants are continually disappearing and being replaced by other individuals of the same species.

A parallel series of problems, though some of them are in detail very different, is provided by the sea coast. Here we have on the one hand sea cliffs, composed of different kinds of rock, all of which are being eroded, not only by rain but by the sea, fast or slowly, and are inhabited by certain species of plants, forming various communities. These have, as a matter of fact, been very little studied, but they appear to have a good deal in common. On flat coasts, on the other hand, we have salt marshes, sand dunes and shingle beaches, where new soil is being accumulated, each type of habitat presenting separate successional and strictly ecological problems. Each of the three may show a straightforward development from the first colonisation of the new habitat, or this may be modified by continual silting with salt mud, continual covering with blown sand, or accretion of fresh shingle; or the habitat may be destroyed at any stage by tidal or wind erosion and the succession started afresh. Or again, the geodynamic factors of tidal or wind action may balance one another and maintain a condition of equilibrium between accretion and erosion, and thus a constant type of vegetation.

CHAPTER XIV

Edaphic Factors. The Soil

EDAPHIC factors are those due to the soil in which the plant is rooted, and it is usually easy to draw a line between these and climatic factors, though, as we have already seen, the characters of the soil are largely dependent upon climate. For example, the soils of a desert are very different from those of a region of high rainfall well distributed through the year, even if they are derived from lithologically identical rocks.

RELATION OF CLIMATE AND SOIL: A HYPOTHETICAL CASE.—Suppose a well-developed bed of limestone of uniform constitution and with a uniform dip is exposed for many miles across country, and that the climate changes steadily as we pass along the strike of the bed. At one end let us say there is an annual rainfall of 5 inches, at the other of 80 inches—and this is not at all an impossible supposition, for extreme changes of regional climate within 100 miles, or even much less, are well known, though they are not common (apart from high mountains) in Western Europe. In the tropics the low rainfall end would be very arid desert, with an exceedingly sparse vegetation of plants highly adapted to scarcity of water. The high rainfall end would bear tropical rain forest, the most complex and highly developed vegetation in the world. The soil of the two ends would be totally different, though derived from identical rock. In the desert the rock would be largely bare, and what soil there was would consist of rock particles disintegrated by heat and wind. In the region of high rainfall there would be disintegration of the rock to some depth, and the comparatively deep soil would be covered by and partly mixed with a layer of humus, and would constantly retain a considerable amount of moisture.

If the outcrop of limestone were accompanied on each side

by parallel uniform beds of very different lithological nature, for instance by sandstone and alluvium respectively, also extending into the two extreme climatic regions, it is probable that at neither end of the climatic scale—neither in the desert nor in the rain forest—would the different beds show any fundamental difference of vegetation. The extreme climatic factors would dominate the situation in each case. In the desert the few species which could just establish themselves in the extremely arid conditions would mostly be able to exist, whatever the chemical nature of the soil, and only some local physical differences of habitat, such as those presented by rock clefts or sand dunes, would cause a differentiation of the vegetation. In the rain forest the very favourable conditions of plant life would enable a very great number and variety of species to exist, and the particular selection present would be determined in the first place by the climate and secondly by the structure of the forest, though differences of soil would have some influence in differentiating plant communities. The climate and all the various soils produced by the different rocks would allow a large margin over the barely necessary conditions of existence.

But in the intermediate region, especially if the rainfall were unevenly distributed during the year, as it usually is, so that there were wet and dry seasons, the difference of the underlying rocks and of their reactions to the climate and to the vegetation would probably cause a marked differentiation of the vegetation. With a 20 to 40 inch rainfall in temperate regions, and an even higher rainfall in the tropics, the limestone soils would tend to be dry and shallow, and the chemical effect of the lime on the soil would also affect the vegetation in more than one way, while adjoining soils might be almost constantly moist. Here then the edaphic factors would be master factors, because they would differentiate the plant communities inhabiting the soils on the different types of rock.

THE SOIL

In recent times the study of the soil as such has become a separate branch of science, now generally known as *pedology* (Greek πέδον, *pĕdon*, the ground, soil). It is only within the last half century that the immense complexity of the processes that take place in the soil and their profound effect on plants have been at all fully realised.

It is impossible here to do more than give a brief account of some of the features of soil, of different kinds of soil, and of their relations to vegetation, which the field ecologist will encounter.[1] There is considerable difficulty in doing even this satisfactorily, because pedology is developing very rapidly and we are still largely ignorant of the *exact* ways in which different soils affect plants. Investigation of these questions leads straight to some of the most difficult problems of plant physiology and physical chemistry.

DEFINITION.—The soil may be defined as the superficial skin covering the earth's crust, created and continuously affected by surface agencies, primarily by the "weathering" agencies —heat, frost, wind, and above all water—acting upon the rocks from which the soil is derived and continuously upon the soil itself; and also essentially affected (and sometimes created, as in peat soils) by the vegetation which grows upon it. This continuing action of surface agencies naturally tends to the development of *stratification*, i.e. the differentiation of distinct layers of soil, from the free surface down to the unaltered present rock, which is a conspicuous feature of practically all *natural*[2] soils.

For the student of vegetation the soil is the surface material of the earth in which plants grow, containing the underground

[1] For the titles of books on the soil useful to the beginning ecologist, see the list of books and papers, p. 238.

[2] Agricultural soils, which are regularly ploughed, and profoundly modified by this and other agricultural operations, do not of course show stratification, because the surface layers turned by the plough are continually being mixed, so that the whole is kept fairly uniform down to the level which the plough reaches.

parts of the higher plants as well as algae, fungi and bacteria—often called the *soil flora*—and also a *soil fauna*, which may be very rich and varied where the conditions of life are favourable, ranging from Protozoa to different kinds of worms, insects and other invertebrate animals, and including small mammals, such as moles, mice and voles, which spend a great part of their time below ground. Surrounded by the mineral and the dead organic constituents (*humus*) of the soil, and by the air and water it contains, these various living organisms form a veritable microcosm at any spot—a little world, with its own atmosphere and water supply, in which chemical, physical and biological changes are constantly going on; and the different elements of this microcosm, especially in a mature and stable soil which has arrived at a state of approximate equilibrium, shows a very complex system of mutual relationships.

The Inorganic Framework

(1) Chemical Characters.—The basis of the great majority of soils is the collection of inorganic particles produced by disintegration (weathering), both physical and chemical, of the parent "rock," either the hard rocks—igneous or metamorphic, or sedimentary grits, sandstones or limestones—or the softer shales, clays and alluvia. Besides these inorganic particles, an organic constituent (humus) is nearly always present. According to the particular rock from which the soil is derived the nature of the soil particles is different, both chemically and physically, but the main inorganic chemical substances forming the basis of soils are three—complex alumino-silicates, silica and calcium carbonate. The alumino-silicates are ultimately derived from such rock-forming minerals as the felspars, hornblende, augite and mica of igneous rocks, which pass into the sedimentary rocks by erosion, transport and redeposit, generally through the agency of water. The silica comes largely from the quartz of acidic igneous rocks and from sandstones. Calcium carbonate, on the other hand, comes mainly from limestones originally

formed in bygone seas by such organisms as corals, foraminifera and calcareous algae. With the alumino-silicates are associated various elements which form basic (alkaline) salts such as calcium, magnesium, potassium and sodium—all except the last being essential elements in plant nutrition. Iron salts are practically always present—iron being an essential element in the formation of chlorophyll—and the oxidation from ferrous to ferric salts during weathering gives the brown or red colour of many soils. Besides these basic elements, phosphorus and sulphur, usually in the form of phosphates and sulphates or the corresponding acids, are always present and essential to plant life. Nitrogen, which is an essential constituent of plant proteins, is mainly derived from humus, but also partly by fixation of the free nitrogen of the air. Traces of other elements also, such as boron and manganese, which have recently been shown to play a vital part in most plant life, though in extremely minute quantities, are found in most soils,[1] and others again are frequently absorbed by plants but probably do not affect their vital processes.

The alumino-silicates form the centre, so to speak, of the essential process of chemical weathering in soil. The originally very complex silicates are broken down, largely by hydrolysis, and the bases removed in solution, while a part of the silica is separated from the complex silicates. The residue is still essentially a complex alumino-silicate, which may vary considerably in chemical composition and physical properties, some of it forming the very fine particles of colloidal clay. This colloidal clay, together with the colloidal humus derived from the decomposition of dead vegetation (see below), forms a *colloid complex* whose components are so intimately associated that it is difficult to separate them without materially affecting their physical and chemical properties, and this clay-humus complex, called the *weathering complex* by pedologists, is the main *reactive* part of the soil, i.e. the part within which the

[1] Besides boron and manganese, cobalt, copper, molybdenum and zinc are among the "trace-elements" affecting the metabolism of plants.

main chemical processes occur. It has the power of adsorbing basic ions from solution, so that its composition and properties depend on the kind and concentration of the ions present in the soil solution with which it is in contact, and these ions are the main proximate source of the mineral food of plants in natural soils.

Calcium is the dominant basic ion in the soil and when present in quantity it imparts physical and chemical stability to the whole weathering complex, aggregating the fine colloidal particles into *compound particles* and thus giving a granular or "crumb" structure to the very fine-grained clays which, without calcium, are unfavourable to many forms of life.

While the calcium ions are thus the great stabilising agent in soil, the free hydrogen ions, derived from the ionisation of acids, promote chemical change. These are the active agents in the chemical action of acids, and in soil are derived mainly from the carbonic acid dissolved in soil water, from the organic acids of humus, and from other acids produced as the result of chemical changes. The concentration of hydrogen ions in a solution is measured by what is called its *p*H value. *p*H is the electrical potential (*p*) of the solution and is expressed by the negative index (exponent) of 10, the quantity so represented being the number of free hydrogen ions in gram-equivalents per litre. Thus, *p*H7 means $10^{-7} = 0 \cdot 0000001$, which is the number in pure water, derived from the ionisation of the molecules of H_2O. When an acid is added some of its molecules are ionised and the number of free hydrogen ions thus increased. *p*H6, for example, means 10^{-6} or $0 \cdot 000001$ concentration of hydrogen ions, ten times that of pure water. *p*H3 $= 0 \cdot 001$ or ten thousand times that of pure water. Thus the lower the negative index (*p*H value) the higher the acidity, each diminution of the value by an integer (representing the negative index) indicating a multiplication of the hydrogen ion concentration by ten. *p*H values above 7 indicate alkalinity of the solution.

There are various ways of measuring the soil reaction. By

far the best is direct determination of the electrical potential, using glass electrodes, but the method of *colour indicators*, employed with proper precautions, gives useful results. This depends on the colour changes of certain organic dyes, whose colours are known to change in definite ways according to the reaction of a solution to which they are added. A selection of these dyes (colour indicators) each of which assumes a certain range of colours through a corresponding range of known acidities and alkalinities, is used for the purpose. A brief description of the use of this method in the field is given in McLean and Cook's *Practical Field Ecology*, p. 94. A full description of the various techniques for determining soil reaction will be found in C. S. Piper's *Soil and Plant Analysis*, Part I, Chapter 2.

Most British soils, except limestone soils saturated with calcium carbonate, those derived from certain basic igneous rocks, and saline soils, are more or less acid in reaction, even if the rock from which they were derived was alkaline. Percolating rain-water, containing excess of hydrogen ions, is active in "leaching" (washing out) basic salts from the upper layers, and the results of this process are particularly marked in the west and north-west where the rainfall is heavy and the rocks are mostly poor in bases to begin with. It is said that the *average* *p*H value of northern English soils under natural vegetation is about 5, which means that the average soil is distinctly, though not excessively, acid.

It must not, however, be supposed that because a soil is distinctly acid in reaction it is necessarily poor in basic ions. Such a soil may be quite destitute of free calcium carbonate, to which basic reaction in soils is usually due, and yet quite rich in calcium ions adsorbed by the colloids of the weathering complex. Thus it has been shown that many of the loam soils of the Chiltern plateau, which are decidedly acid, with a *p*H value of between 4 and 5, have a high "base status,"[1] and

[1] The term "base status" is commonly used to apply to the concentration of *cations*, the metallic ions of the basic salts, rather than to the salts themselves.

they support finely grown beechwood and other luxuriant vegetation. On the other hand extremely acid soils, with a *p*H value of between 3 and 4, are in fact very poor in bases and support only a specialised (basifuge or oxyphilous) natural vegetation of plants like heather, mat grass and wavy hair-grass. These are the soils called "sour" by agriculturists, and they need the addition of lime to render them fertile. On agricultural land sour soils bear characteristic weeds like sorrel and spurrey. The differences between them and fertile soils cannot be fully understood without reference to the humus content of soils (see p. 183).

(2) Physical Characters of Soils: Soil Texture.—The nature and size of the mineral particles constituting the inorganic framework of soils not only influence the chemical processes, but directly determine the physical nature of a soil and its effect upon plants. The *texture* of a soil depends primarily on the sizes of its mineral particles (though its actual structure is much modified by crumb formation and by humus), and this feature is of great importance to plants because it controls aeration, water-holding capacity and the ease with which water can traverse the soil. The proportion of particles of different sizes present in a soil is ascertained by the procedure called *mechanical analysis*, in which the *fractions* of the soil whose particles lie between different limits of size are determined. To these fractions the common names of well-known types of soil—gravel, sand, silt and clay—are applied. The agreed international standards of size of the different categories are as follows:—

Gravel (and stones)—particles above 2 mm. in diameter
Coarse sand—particles from 2 to 0·2 mm.
Fine sand—particles from 0·2 to 0·02 mm.
Silt—particles from 0·02 to 0·002 mm.
Clay—particles below 0·002 mm.

All soils contain in fact particles belonging to more than one of these categories, the soil itself being named after the fraction

which is preponderant. When soil consists of a good mixture of particles of widely different sizes with an adequate humus fraction it is called a *loam*.

In mechanical analysis a sample of air-dried soil is first heated to 100° C. in an oven till it no longer loses water, and then heated to redness in a crucible or on a sheet of metal to burn away the humus. The mineral residue is then pounded in a mortar to reduce it to its elementary particles, and washed through a series of sieves, each with a mesh of definite diameter, to separate the coarser particles, and the successive fractions dried and weighed. This procedure of course destroys the *structure* of the soil by breaking up the compound particles or "crumbs," so that it only gives information as to the proportions of the ultimate mineral particles of which it is composed.

A rough qualitative analysis of a sample of soil can be made by shaking up 10 grams in a large jar of distilled water. The sand fractions sink in a few minutes, the silt in the course of a few hours, while the fine clay remains suspended in the water indefinitely. After the sand has sunk the turbid liquid may be carefully decanted off and distributed among several jars which are then filled up with distilled water and left standing. The rate of settling and the final turbidity of the water will then give a good rough idea of the proportions of the silt and clay fractions. A pinch of washing soda added to the water aids dispersion and thus separation of the particles.

Characters of Soils of Different Textures

Gravels are soils with a preponderance of large particles above 2 mm. in diameter,[1] practically always mixed with a coarse sand fraction and some finer particles as well. Aeration and percolation of water are extremely free. Gravel soils are unfavourable to plant life because of their dryness and poverty

[1] "Stones" are usually reckoned as fragments above 3 mm. (or even 4 mm.) in diameter, but sometimes all the gravel, i.e. particles above 2 mm. are reckoned as "stones."

in nutrients, unless the ground water is high and carries nutrient salts. A gravel soil has the characters of a coarse sand in extreme form.

Sandy soils have a preponderance of particles between 2 mm. and 0·2 mm. in diameter (coarse sand) and between 0·2 mm. and 0·02 mm. (fine sand). The particles are typically of silica (SiO_2). Percolation of water and aeration are free, the water-holding capacity (in default of abundant humus) and power of raising water slight, because the spaces between the particles are too wide. Hence sands are dry soils unless the ground water is high, and warm, "early" soils because, owing to their dryness, they warm up quickly in spring. They are light and easy to work but typically poor in nutrients because of the deficiency in the finer particles with which the bases are associated, and because the free percolation of rain-water leads to very thorough leaching. For this reason they are easily "podsolised" (see p. 188) and quickly develop acidity.

In oceanic and suboceanic temperate climates sandy soils often bear heath or heathy woodland, characteristically of birch and pine, with a tendency to the formation of raw humus (*mor*, see p. 185). Sandstones with sufficient of the finer fractions to maintain their base status develop the "Brown Earth profile" with mild humus (*mull*, see p. 184) and support deciduous summer forest, though coarse sand grains may be abundant in the soil and affect the nature of the subordinate vegetation. Deforested soils of this nature tend to podsolise and develop heath, though they make good agricultural soils for certain crops. Coastal blown sands support a specialised vegetation adapted to cope with their mobility (p 74-5). On stabilisation they resemble sandy soils derived from coarse sandstones and tend to develop heath.

Silt soils are intermediate between sands and clays in the size of their particles. They are favourable soils for vegetation because they have considerable water-holding capacity, while percolation, aeration and capillary rise of water are fairly free. The name is derived from the prevalent texture of alluvial soils

(silts) laid down on the flood plains of rivers. These soils probably originally bore alder and oakwood, but have mostly been converted to meadowland. Near large towns silt soils have been much used for market gardening.

Clays are soils in which the particles below 0·002 mm. in diameter, typically of hydrated alumino-silicates, are numerous enough to give character to the soil. Any soil with a proportion of 30 to 40 per cent or more of these fine particles would be called a clay soil. Clay soils have all the qualities opposite to those of sand: percolation of water is very slow or almost nil, aeration defective, and water-holding capacity very high. Clay soils are wet (often water-logged for long periods in winter), heavy, difficult to work, cold and "late" because they warm up slowly owing to the high water content. Under continued drought the clay colloid shrinks, cracks, and eventually "bakes" hard. These characters make clay soils physically unfavourable to many plants, and root systems tend to be shallow because of the difficulty of adequate aeration at greater depths. This effect can be well seen on clay grassland, where the grasses are all shallow-rooting species, and in clay woods, where the roots of shrubs and trees tend to be concentrated in the "improved" surface soil, failing to penetrate the unaltered clay below, while in a sandy wood the roots of the woody plants are more spaced out vertically and reach a greater depth. On the other hand clay soils are often chemically favourable to plants because they may be rich in bases associated with the complex silicates, the basic ions free or adsorbed by the weathering complex. Clays are, however, sometimes deficient in essential nutrients, e.g. phosphates, and sometimes in bases also. Clays are much improved by an abundance of mild humus (mull) which "opens" and lightens the soil, and by calcium carbonate which flocculates the clay colloids so as to form "crumb structure" and secures better aeration and freer movement of water.

Clay soils in the midlands, south and east support typical damp oakwood. After deforestation they have been largely converted to "permanent grass," which is, however, unprofitable

when not carefully tended. Much of this clay country was formerly arable and produced good wheat, but when labour costs are high and the price of wheat is low, the heavy clay soils do not pay for the cultivation required.

Loams, consisting of a good mixture of particles of different sizes, are the most favourable soils for the great majority of plants because they tend to combine the good qualities of the extreme types. Thus the clay and humus fractions give consistency and water-holding power and supply plant food, the particles of medium size permit of the capillary rise of water, while the sand particles facilitate aeration. The constitution of loams has a wide range according to the relative preponderance of one fraction or another: thus we have "heavy (clay) loams," "medium loams," and "light (sandy) loams." With an adequate supply of bases, especially calcium, plenty of mild humus and good water supply and drainage, medium loams are the ideal soils for all plants except highly specialised types adapted to extreme edaphic conditions.

Limestone Soils.—Soils derived directly from limestones form a class apart. A relatively pure limestone like the chalk (often 90 per cent, and in some cases nearly 100 per cent of which consists of calcium carbonate), weathers by chemical solution of the carbonate, not primarily by mechanical erosion, though this may contribute where the rock is exposed in cliffs and scars. For the most part gradual solution of the rock takes place below the carpet of vegetation and surface humus through the action of percolating rain-water containing carbonic acid. The result is the formation of a shallow soil consisting of the scanty residue of insoluble mineral particles and of surface humus, the whole saturated with calcium. This is the type of weathering which occurs on the grass-covered slopes of the chalk downs and of the older limestone hills of the north and west, and also below the leaf litter and abundant humus of the beech "hangers" on chalk escarpments and valley sides. Such shallow limestone soils are dry soils, because the percolating rain-water quickly escapes through the fissures of the rock below.

They support a herbaceous vegetation of plants which can tolerate drought, including species ("calcicoles," see p. 195) which flourish on alkaline soils and cannot tolerate acid conditions (see also p. 193 under *Rendzinas*).

Deeper soils are, however, formed from limestones which contain a larger proportion of insoluble mineral particles and also, though much more slowly, on flat horizontal surfaces of almost pure limestones like the chalk, where the very scanty insoluble constituents derived from a great thickness of dissolved rock have had time to accumulate in depth and are not removed by rainwash down a steep slope. Under such conditions the nature of the resulting soil depends on the nature of the insoluble material of which it is composed. If this is largely clay or silt, a good water-holding soil is produced, if it is largely sand, a light permeable soil.

(3) The Organic Fraction of the Soil: Humus.—Practically all soils contain organic material derived from the disintegration of plants or parts of plants such as dead leaves, roots and rhizomes, with a small addition from animal excreta or dead bodies. Apart from highly exceptional soils, such as those accumulating below maritime "bird cliffs" or "bird rocks" inhabited by thousands of sea birds, which are largely formed of the birds' droppings, the animal contribution is insignificant compared with the great bulk of plant material. The term *humus* is usually applied to the whole complex of disintegrating and decaying organic material in or on the soil, but sometimes it is restricted to the brown substance, soluble in acidified water, which is formed as a late result of the processes of disintegration and chemical change of the organic debris. Here it will be used in the former sense. Dead leaves and stems lying on the surface of the soil, before they disintegrate, are distinguished as *litter*. The soils of habitats such as deserts, in which the vegetation is always sparse, and new soils, freshly formed from inorganic material, contain the least humus, mature well-vegetated soils the most.

In a raw soil, freshly formed from rock or alluvium, humus

begins to accumulate directly plants of any kind settle upon it, and a certain contribution may also be made by windborne particles of organic substance. In many soils earthworms are important agents in incorporating dead leaves and stems with the soil. They drag them down into their burrows, and constantly pass large quantities of humus through their bodies, disintegrating and partially digesting the organic matter. They are aided in the work of disintegration by other small soil animals, and also by soil fungi and bacteria. Eventually the disintegrated and decomposed organic substance is finally broken up by bacteria of different kinds into carbon dioxide, water, and simple salts, which break up in water into anions and cations, the latter mainly of calcium, magnesium and potassium, the former containing nitrogen, sulphur and phosphorus, all of which elements are necessary ingredients of plant food. A most important chemical soil process as regards the food of the higher plants is *nitrification*, the conversion of ammonium salts into nitrites and then into nitrates, the last process being carried out by the so-called *nitrifying bacteria*. The great majority of green plants absorb their nitrogen in the form of nitrates. These processes take place most freely and rapidly in soils with a fairly high "base status"[1] and a moderate water content, in the presence of plenty of free oxygen and at a moderately high temperature, i.e. in rich, moist, warm, well-aerated soils. This is because these conditions are most favourable to the life of the organisms which carry out disintegration and decomposition, from earthworms down to the aerobic nitrifying bacteria.

The kind of humus formed where the processes described are free is known as *mull* (mild humus). Under these conditions the *humus turnover* is quick when the temperature is sufficiently high. Humus is formed in quantity, and rapidly, because the favourable conditions for the growth of plants give an abundant supply of plant material, and this is rapidly decomposed because

[1] That is soils containing a good supply of cations, not necessarily of alkaline *salts*.

of the favourable conditions for the activity of the soil organisms. In this way an ample supply of the ions of the mineral salts which had been locked up in the plant tissues is set free and made available again as plant food. Mull is therefore characteristic of the fertile soils of high base status already described. It is well incorporated in the soil and becomes combined with the compound particles of colloid clay to form the reactive weathering complex.

At the other extreme is the type of humus known as *mor*, formed in less favourable life conditions under which it tends to accumulate and becomes very acid in reaction. There are several conditions leading to the production of mor. First it tends to be formed in soils derived from rocks which are very poor in bases, such as many of the siliceous rocks of the north and west of Britain and some of the sandy soils of the south and east. Secondly it is formed especially in a cold damp climate where the conditions are unfavourable for the active life of many of the mull-producing soil organisms. Thirdly, high rainfall leads to thorough leaching of the surface layers of soil, carrying down the soluble mineral salts to lower layers, especially quickly on highly permeable soils, and thus increasing the poverty of the upper layers and leading to the formation of mor. Where one or more of these conditions prevails the formation of humus from litter is slowed down and partly decomposed litter tends to accumulate, becoming highly acid because the bases contained in the decomposing plant substances are leached out and the organic acids are not neutralised. The excess of hydrogen ions renders the humus substances extremely mobile, and heavy rain carries them down to lower levels, especially in a permeable soil. The solubility and consequent mobility of mor humus are conspicuously shown by the brown colour of moorland streams draining from acid peaty soils, especially when the streams are in spate. In the hilly and mountainous regions of the west and north of Britain all the conditions leading to the production of mor—siliceous rocks poor in bases, a cool damp climate and heavy rainfall—

are frequently combined, so that mor soils are the prevailing type over wide areas.

The soil fauna and flora of mor are totally different from those of mull. Earthworms and other invertebrates active in the formation of mull are absent, and instead of the wide range of bacteria, including the nitrifying bacteria, present in mull, certain fungi, especially Hymenomycetes, are the predominant "saprophytic" forms of lower plant life. The absence of nitrifying bacteria means that no nitrates are produced, and ammonium compounds are the main form of combined nitrogen available for the nutrition of the higher plants. The mor soils with complete absence of nitrates are found by Pearsall to have a *p*H value below 3·8, which appears to be a critical limit separating mor from mull in several soil series; but there are soils less acid than this which show at least incipient mor formation and may be transitional between the two types.

The deficiency in bases characteristic of mor can be readily tested in the field by shaking up a sample of the soil with Comber's reagent for "sour" soils—potassium or ammonium thiocyanate in saturated alcoholic solution. Ferric iron comes into solution from the resulting base exchange and red ferric thiocyanate is formed only if bases are deficient. The intensity of the red colour produced thus serves as a measure of the "degree of unsaturation by bases." If ferrous iron is also present this can be converted into the ferric state by exposure to air or by the addition of one drop of hydrogen peroxide—a strong oxidising agent—to 10 c.c. of the solution, and the depth of the red colour is then increased in base-deficient soils.

Water Content of Soils.—The amount of water contained in a given soil at any moment depends upon several factors. We have seen that the water relations of soils of different textures are very different, the amount of water retained by the soil depending on the size of the soil particles and the amount of humus present. Water percolates very readily through gravels and sands, which are mainly composed of coarse particles, because of the large air spaces between the

particles. The smaller the particles, and consequently the air spaces, the slower the percolation and also the longer the soil takes to dry. Very small particles or fine spongeworks such as make up the colloids of clay and humus also hold the water strongly because of another force—the tension brought into play by the immense aggregate surfaces of the microscopic particles or meshes. A clay holds water very strongly indeed, so that the plant roots themselves cannot extract from it nearly all the water present. Humus is also a very important water-holding constituent and soils rich in humus retain a considerable amount of water, which they absorb and hold like a sponge for a long time, even in relatively dry air. The result is that much less water is required to saturate sandy soils than clay and humus soils and sandy soils retain much less under the same evaporating power of the air. Similarly plants can use nearly all the water in sand but not nearly all that held by clay.

In considering the supply of water to the soil we must distinguish between ground water and water coming directly from rainfall or held in the surface layers. *Ground water* is water derived from a more or less permanent "water table." In lakes and rivers this is above the soil surface, in a marsh at or very close to the surface, in many alluvial soils but a short distance below. Underground water may be close to the soil surface when there are underground streams or bodies of water held up by an impermeable stratum below. Thus a thin surface stratum of sand or gravel may be kept constantly moist because it lies over a clay stratum just below. But very often the water table lies so far below the surface that it has no effect on the surface soil, which then depends for its water-content entirely on direct precipitation. After heavy rain of course this increases very much, saturating the surface layers, while the excess above the saturation point runs off or percolates through to lower layers. Evaporation begins, but is retarded by a damp and stopped by a saturated atmosphere. During a long spell of hot weather or of drying winds, when the saturation deficit of the air is high, evaporation decreases the water in the surface layers

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of soil so that they become "air-dry."[1] A close vegetation cover greatly decreases direct evaporation from the soil surface, but a soil may lose water more rapidly by absorption through the roots of the plants and evaporation (transpiration) from the much more extensive aggregate surfaces of the leaves, than directly by evaporation from the soil surface, so that a heavy carpet of vegetation tends to dry out the soil.

"World Groups" of Soils

Brown Earths and Podsols.—We have seen that the cool damp climate of the north and west of Britain is one important factor leading to the formation of "mor" soils, while the warmer and drier climate of the south and east is more favourable to the production of "mull." This contrast is an example of the differentiation of soils by climate which has led to the recognition of what pedologists call "*world groups*" of soils, dependent primarily on climate. The two world groups represented in Britain are called respectively *Brown Earths* (or Brown Forest soils) characterised by relatively high base status, the presence of nitrates, and the formation of mull, and *Podsols* by low base status, the absence of nitrates and the formation of mor. The brown colour of Brown Earth is due to hydrated ferric oxide derived from iron-containing alumino-silicates in the parent rock and liberated in the weathering complex. "Podsol" is a Russian word meaning "ash," from the pale ash-colour which often marks the layer immediately below the dark surface mor of the typical podsol (see p. 190).

We saw at the outset that stratification, due to the continuous action of surface agencies, is a feature of nearly all mature natural soils. This stratification gradually develops in a newly formed soil until, in a mature soil, the whole depth of stratified

[1] Soil is said to be "air-dry" when the tension of the water held by the soil is in equilibrium with the tension of water vapour in the air, so that evaporation stops. Theoretically of course a soil is "air-dry" when it is saturated with water in contact with a completely saturated atmosphere. But in practice the term is used only if the soil is in contact with air of the average humidity of a dry room or in dry weather out of doors.

soil (called by pedologists the *soil profile*) down to the subsoil or parent rock, has attained a condition of equilibrium. In regions of moderate and high rainfall the primary agent of stratification is the percolating rain-water and its interaction with soil constituents, both mineral and organic. The descending water has two main effects. First it washes down fine particles from the surface to lower levels, and secondly it dissolves soluble salts and carries their ions downwards, frequently redepositing salts at a lower level. The result of these actions of percolating water is the impoverishment of the surface layer of the soil in fine particles and in bases, and their accumulation in lower layers. Thus we can distinguish in mature soils an *eluvial layer* above from an *illuvial layer* below, generally known by pedologists as the *A* and *B horizons*. These distinct "horizons" are well illustrated in Brown Earths and even more sharply and conspicuously in Podsols.

Brown Earths are best studied in natural or semi-natural deciduous woodland which has been undisturbed for a long time. They are most typically developed on a clay or loam subsoil, but are also formed on sandstones and limestones containing a large clay or silt fraction. The profile of a typical Brown Earth is free from calcium carbonate, any that was derived from the parent rock being leached out by percolating rain-water and either ionised in the soil water, the Ca ions entering the weathering complex, or carried down to lower levels together with the finer clay particles. The whole profile is usually somewhat acid with a gradient of decreasing acidity and increasing salt content downwards. The *A* horizon (eluvial) has a good proportion of finely divided mull well incorporated with the mineral constituents, and a relatively high base status, the basic ions, including calcium, being held in the crumb structure of the weathering complex. The *A* horizon is relatively well aerated and has a rich microflora and fauna, with the presence of earthworms. The *B* horizon is often not sharply delimited and passes down gradually into the unweathered parent clay or loam.

Sometimes the surface layers have a higher *p*H and a higher salt content than the lower, owing apparently to the carrying *up* of salts in the plants themselves, whence they pass to the humus through leaf fall, or by the capillary rise of soil water in dry weather. There seems in fact to be an alternating movement of water in many of these soils, downwards in wet weather and upwards in dry, when evaporation exceeds precipitation. This tends to maintain the stability of the Brown Earth profile and to prevent podsolisation, which is associated with a "one way" (downward) movement of water. In general the *p*H value obtained depends largely on the proportion of soil to water and on the salts present in the soil. Soil samples taken in spring or early summer, when nitrate concentration is high, will show a lower *p*H value than those taken in winter when the soil is wetter.

Most of the good agricultural land of Britain is of the Brown Earth type, but ploughing of course destroys the stratification and tends to make the soil homogeneous to the depth to which the plough reaches. Manuring is necessary to replenish humus and to maintain the base status, since the plant material, which in a woodland is constantly supplied to the soil through leaf fall, is removed with the crop, together with its contained salts. Artificial manures maintain base status without replenishing humus.

Podsols, with their "mor" humus, are characteristic, as we have seen, of the cool wet climates of the west and north, where precipitation exceeds evaporation for most of the time, and consequently the downward movement of water is on the average much stronger than the upward. Under such conditions leaching and eluviation are extreme. The prevailing lower temperatures check the disintegration of plant debris and a layer of highly acid raw humus (mor) tends to form on the surface of the soil. This is called the A_0 horizon, since it is an added stratum above the mineral soil. Below the surface mor comes the *A* horizon proper, very poor in basic ions, often grey or even white in colour, but sometimes stained chocolate

brown by the humus substances carried down from A_0 by the acidified percolating water. Then we come to the illuvial horizon, sharply marked in a typical podsol, often in two distinct layers—an upper layer (B_1) in which humus substances are precipitated and a lower (B_2) in which ferric salts accumulate. B_1 is commonly dark chocolate brown or nearly black, B_2 reddish brown. Either or both may be cemented into a hard layer, the so-called "moor pan" or "hard pan," which may be thick and resistant enough to stop the downward growth of tree roots and prevent their penetration to the richer subsoil, confining the roots to the impoverished A horizon. Foresters have to pierce or break up hard pan when planting on such a soil or the planted trees cannot make good growth.

In a "podsol climate" podsols may be formed from almost any parent material, though rarely on limestones or highly basic igneous or metamorphic rocks, which provide an alkaline buffer as the rock is dissolved by carbonated rain-water, so that acidification of the surface soil is prevented. On flat limestone surfaces in a sufficiently cool damp climate raw humus may be formed from lichens and mosses colonising the surface, and in this heath-plants may germinate and take root, but a considerable thickness of insoluble residue must accumulate before a soil which can be podsolised is formed. In the warmer climates of the south and east, with their lower rainfall, podsols are commonly formed only on coarse sands and gravels of low base status, but these are frequently very well developed and show typical B_1 and B_2 horizons, whereas in the non-sandy soils of the podsol climate so-called "iron podsols," in which B_2 alone is formed, commonly occur.

It must be emphasised that well-developed Brown Earth and Podsol profiles are only to be found in undisturbed mature natural soils where the conditions are favourable. There are many factors which may prevent or destroy the typical stratifications described. Apart from destruction caused by ploughing, very many soils are immature, either because they are comparatively recently formed or because they exist under con-

ditions, e.g. on steep slopes, where the soil can never become mature. Then again the surface layers of a mature profile may be destroyed by erosion, for example as a result of deforestation, and the lower horizons exposed. Such "truncated podsols" in which the *A* horizon has been destroyed, exposing the *B* horizon on the surface, are not uncommon.

Local Soil Types

Besides the two main "World Groups" occurring in the British Isles and apart from the disturbed, eroded and immature soils just mentioned, there are various other soil-types which are formed under definite local conditions.

Meadow Soils.—Meadow soils occupy flat ground with a fluctuating water table never very far below the soil surface. Typically this ground coincides with the alluvium of river valleys and is grassland traditionally cut for hay, but now often used as permanent pasture. This riverside alluvium is subject to winter flooding which brings fresh silt to its surface and maintains its fertility. The meadow soils are in fact often rich in bases and very fertile. Flooding of the alluvial grasslands is now usually regulated or prevented by dredging of the river beds, by embankment, by the cutting of drainage ditches, and by regulation of the water flow through sluices, but the ground water does not lie at any great depth. With a persistently high water table nearly reaching the surface and causing water-logging, marsh plants tend to increase in abundance, but the true meadow soils are not deficient in oxygen owing to the constant rise and fall of the water. Impeded drainage and relatively high but fluctuating water-level are the characteristic features of meadow soil. The abundant humus, largely derived from the numerous fine roots of the grasses, remains near the surface and the underlying mineral soil is grey or blue-grey in colour. If this kind of soil is thoroughly drained so as to lower the water table considerably, leaching of the surface layer begins and the soil tends to develop the Brown Earth profile.

PEAT SOILS.—When soil is constantly water-logged and the water is relatively stagnant, oxygen is permanently deficient, and in the absence of silting humus constantly accumulates and never disintegrates completely, thus forming a pure coherent organic soil or *peat*, often of great thickness. If the water has drained from calcareous or other basic rocks typical *fen peat* is produced, rich in bases, especially calcium, with a *p*H value between 7 and 8. This is formed in shallow "fen basins," of which the largest British example, now practically all drained and cultivated, is found in the East Anglian Fenland between Cambridge and the Wash. Undrained fen bears characteristic fen vegetation dominated by various reeds, rushes and sedges. If the plant debris accumulates so as to rise above the influence of the basic ground water, oxyphilous plants, notably bog moss (*Sphagnum*), settle down on the fen and form peat which is no longer saturated with calcium. This may serve as starting point of the formation of a *Raised Bog*, in which a kind of peat very different from fen peat, very poor in bases, acid in reaction and inhabited exclusively by oxyphilous plants, is produced. This acid *bog peat* is also formed in local depressions of heaths or moors, at the bottoms of moorland valleys where drainage is impeded (*Valley Bog*), and over wide tracts of flat low-lying country and on mountain plateaux where drainage is poor, rainfall of long duration, and the air almost constantly damp, so that the P/E ratio is persistently high (*Blanket Bog*). Blanket bog peat might indeed almost be reckoned as a climatic soil type since it depends on a decidedly wet climate; but on well-drained areas in the same regions podsols bearing heath, scrub, or even woodland are developed—absence of free percolation and of surface drainage ("run off") being the other essential factor in the formation of blanket bog. If there is free downward drainage through the mineral substratum lying below the bog peat, podsolisation will occur in it and *A* and *B* horizons develop. In such cases the peat may be regarded as an enormously exaggerated A_0 horizon.

RENDZINAS.—Limestone soils form a class apart, as we have

already seen (p. 182), owing to the overwhelming effect of the calcium carbonate of which the rock is mainly composed. On relatively pure limestones such as the chalk they are characteristically shallow and dry. Below the dense dark surface humus a young chalk soil is white or grey and passes down at once into the weathered limestone, the whole profile, including the humus layer, being saturated with calcium carbonate. The *p*H value of a chalk soil is usually between 7 and 8. The unlimited supply of lime below acts as a strong alkaline buffer, lime being constantly brought to the surface by the upward current set up when evaporation is strong, and by soil animals. In such a soil, called a *rendzina*, there is little or no leaching, and the humus is practically immobile, at the opposite extreme from the very mobile humus of a podsol. Consequently no *A* or *B* horizon is formed and the percolating rain-water, saturated with lime, drains away through the fissures of the rock. Such a soil is thus "permanently immature." It is added to from below by the gradual solution of the calcium carbonate leaving behind the insoluble mineral particles, of which even in the purest limestones a certain proportion is present.

In course of time a mineral soil thus accumulates on flat ground where it cannot be carried away by "run-off," and more rapidly of course on impure limestones which contain a considerable proportion of insoluble mineral particles—sand, silt or clay. Ultimately, therefore, a considerable depth of mineral soil may accumulate over limestone in such situations, and leaching begins when the mineral soil reaches a certain depth so that the surface layers are no longer affected by the underlying limestone. The effect of surface leaching may be seen in the so-called chalk and limestone heaths developed on level expanses, alike on the flat summits of chalk downs and on limestone plateaux. These show a curious mixture of species, heath plants settling in the surface humus while calcicolous species are rooted in the calcareous soil below.

Besides these "chalk heaths" extensive areas of the chalk plateaux in the south of England are covered with genuine

heaths dominated by *Calluna* and with no calcicolous plants. These are situated on loams or sands overlying the chalk, sometimes perhaps derived by continued leaching of an original chalk soil, but often composed of or including remains of non-calcareous Tertiary or Quaternary deposits which at one time overlay the chalk. Where these loams are derived from the chalk itself they commonly include many insoluble flints originally embedded in the chalk rock, and they are then generally known as "clay-with-flints," though their nature actually varies from a clayey to a sandy loam.

On the limestone soils of northern regions, where the climate is cold and wet, acid humus often accumulates in the turf of the grassland so that the surface layer becomes acid even close above limestone rock. In such grassland there are commonly a number of oxyphilous plants which do not occur in chalk grassland. In the deeper soils overlying chalk and other limestones there is frequently a layer of loam, brown or reddish brown owing to the liberation of ferric salts, between the surface soil and the unaltered limestone rock; and on some of the older and harder limestones this may show a sharp discontinuity with the rock. British limestone soils still require more thorough investigation.

Calcicoles and Calcifuges

It is well known to all botanists that the flora and vegetation of highly calcareous soils, such for instance as the shallow (rendzina) soils of the chalk downs, are very different from those of markedly acid, base-deficient soils like those of a typical sandy heath or of a peat-covered moor. Many of the species found on calcareous soils rarely or never occur on highly acid soils, and vice versa. These two categories of species have long been known respectively as *calcicoles* and *calcifuges*. There are, however, also a number of species which may be found on both of these extreme types of soil—in the matter of excessive or deficient lime content they are indifferent,

For a long time there was difference of opinion as to whether the characteristic species of limestone soils inhabited them because of the distinctive chemical factor or whether they depended rather on the distinctive physical conditions of limestone soils. It seems probable that both cases occur. But it has recently been shown (Hope Simpson **154**, 1938) that many characteristic chalk species also occurred in quantity on a certain plot of Lower Greensand soil which in the past (probably well over half a century before) had been so heavily limed that its average content of calcium carbonate when the observations were made was distinctly high (4·5 per cent) though not nearly so high as that of a typical chalk grassland soil, which often exceeds 30 per cent. Since the *physical* nature of this lime-containing Greensand soil was practically identical with that of a comparable plot of the normal Greensand soil which contained *no* determinable calcium carbonate (though minute quantities of calcium ions were present) it is difficult to avoid the conclusion that the "chalk plants" present on the lime-containing Greensand are genuine *chemically determined calcicoles*. Among these were such well-known and abundant chalk grassland species as the hairy hawkbit (*Leontodon hispidus*), salad burnet (*Poterium sanguisorba*), upright brome (*Bromus erectus*), and a number of others.

What is it that determines the marked preference of these species for soils containing abundant calcium carbonate? It has nothing to do with the purely nutritional requirement of minute quantities of calcium ions, shared, so far as we know, by all flowering plants. Calcifuges obtain these from the most base-deficient soils. We do not know of any direct beneficial effect of calcium carbonate *as such*, on the plant. Its effects on *soil*, as we have seen, are good in more than one way, but these are secured by much smaller quantities of lime than those present in such highly calcareous soils as those of chalk grassland.

These markedly calcicolous plants are certainly intolerant of acid soils, and from this point of view they might be classed as "acidifuges" or "oxyphobes." It seems probable that a

markedly basic reaction in the soil solution is really favourable to them in some way or another—that in their metabolism they are in fact "basiphils."

Besides the "chemically determined calcicoles" on the plot of lime-containing Lower Greensand soil referred to above there were a number of species, constant in chalk grassland, but also occurring on the normal Lower Greensand soil free from lime. Among these were the two fine-leaved fescues (the sheep's fescue, *Festuca ovina* and the red fescue, *F. rubra*), and such plants as ladies' bedstraw (*Galium verum*) and ribwort plantain (*Plantago lanceolata*). The fine-leaved fescues are the commonest dominants of pastured chalk grassland, but they also occur on other dry soils with little or no calcium carbonate, the sheep's fescue being notably co-dominant with the common bent-grass (*Agrostis tenuis*)—which is on the whole a calcifuge —over very wide areas of rough pasture on the siliceous rocks of the west and north, and on grazed sandy commons in the south. Ladies' bedstraw is far from being confined to chalk grassland, and ribwort plantain is an exceedingly common plant found on a wide variety of soils. These species are certainly not chemically determined calcicoles, though they are abundant on soils containing an excess of calcium carbonate.

When we turn to the typical *calcifuges*, we find a strong intolerance of lime-containing soil water. Of characteristic species belonging to this category the common ling (*Calluna vulgaris*), the wavy hair-grass (*Deschampsia flexuosa*) and the heath bedstraw (*Galium saxatile*) occurred on the acid Lower Greensand but not on the calcareous sand, and they are never found on genuine chalk soils. Many species of bog moss (*Sphagnum*) are so intolerant that lime-containing water directly "poisons" them. Many species of the heath family besides the common ling never occur on calcareous soils, for example the purple bell heather (*Erica cinerea*) and the allied bilberry (*Vaccinium myrtillus*), and the same is true of many bog-plants such as *Eriophorum* ("cottongrass"). Several of these plants have been shown to form considerable amounts

of fatty acids in their metabolism and it has been suggested that the absorption of calcium would lead to the formation in the plant tissues of insoluble calcium soaps, with deleterious results to the plant. Many plants, not necessarily calcifuges, show what is known as "lime chlorosis" when growing on highly calcareous soils, the leaves being pale yellow instead of green owing to inadequate formation of chlorophyll. This may be due to the calcium in the soil water inhibiting the absorption of iron which is necessary for the production of chlorophyll, and also possibly the "trace element" manganese. In others the lime hinders the absorption of potassium—another essential element—between which and calcium there is a marked antagonism. Indeed, there is evidence that what has been called the "basic ratio," i.e. $\frac{Ca + Mg}{K + Na}$ in the soil solution has an important effect on plants and that only where it is high is the soil suitable for those species which have a high base requirement and are intolerant of acid conditions. But we are still far from a thorough understanding of these factors.

Range of Tolerance and Competition

When we consider the great differences between the demands made upon the soil by different species, their different degrees of tolerance of various soil conditions, the great complexity of these conditions, the interactions of different soil factors upon one another, and the modifications of the effects of soil factors by differences of local climate and water supply, it becomes clear that the actual places in which the individuals of a particular species find themselves, i.e. which the seeds can reach and in which they can germinate and the seedlings establish themselves, must vary almost infinitely in their suitability for that species. Some plants have a narrow, some a wide range of tolerance of various soil conditions. Take for example the factor of acidity and alkalinity, i.e. of *p*H value. It has been

shown by careful culture experiments with a number of species that each has a definite range of *p*H value within which it can grow, and a narrower (optimum) range within which it grows luxuriantly. It is obvious that within the wider range, but outside the narrower, the plant is more or less handicapped in its growth and other life functions. The factor of *competition* with other species will now play a decisive rôle. A plant may be able to succeed in a soil of given *p*H value when it is growing alone, but not if this value, with the rest of the factors present, enables surrounding plants to grow more vigorously so that they overshadow and tend to smother it.

An experiment which brings out the point as regards the *p*H factor (or some other factor depending on excess of calcium carbonate) has been made on the competition between two species of bedstraw, *Galium saxatile* and *G. silvestre*, grown together on different types of soil. The former species can tolerate and flourish on acid soils, but if there is an excess of calcium carbonate, the seedlings grow very slowly, suffer from lime chlorosis, and many of them die. Those which survive, however, eventually recover, grow into perfectly healthy plants, flower, and set seed. *G. silvestre*, on the other hand, can tolerate large amounts of calcium carbonate in the soil, and this does not interfere with the rapid growth of the seedlings. Consequently, if the seeds are sown intermixed on calcareous soil, the slowly growing and sickly seedlings of *G. saxatile* are overshadowed and killed by the flourishing plants of *G. silvestre*, even though a few of the former would have survived and grown into healthy plants if the latter species had been absent.

Thus the fact, which we observe in nature, that *G. saxatile* is confined to non-calcareous soils is explained by the fact that it is severely handicapped, though it does not necessarily die, on calcareous soils, and any seedling starting growth on such soils will be killed by the competition of species which are not so handicapped. Similar experiments will help to determine the causes of the distribution of other species, even though the experimenter may be unable to proceed to the investigation of

the physiological causes of the actual effect of the soil on the species, a more difficult problem.

In a neglected garden bed many of the garden plants, which grew very well when they were isolated, are soon smothered by weeds if these are not removed. The weeds have a much wider range of tolerance in many respects and many garden plants are growing under conditions which are not optimal for them, though they succeed quite well in the absence of competition.

Examination of Soils in the Field

A detailed and thorough examination and analysis of a soil, such as a pedologist would make, usually lies outside the range of a working ecologist, though it is important that he should grasp the main facts of soil constitution and structure and be able to recognise at sight the leading types he will meet in the field. When he can do this his main concern is to determine as far as possible the relations of particular soils to the vegetation that grows upon them.

In examining the soil of any area of natural or semi-natural vegetation that is being studied, the first thing to do is to dig a small pit in an apparently undisturbed place, from the surface down to the subsoil, so as to expose the whole soil profile. One side of the pit, at least, should be cut clean and vertical with a sharp spade so that the stratification is not obscured by fragments of the upper layers falling and covering the lower ones. A sketch of the profile drawn to scale should now be made, with full notes of the general appearance, colour and texture of the various horizons. In this sketch the positions of the underground parts—rhizomes and roots—of the different plants growing on the surface should be indicated. This preliminary examination of the profile cannot be too carefully carried out, for it furnishes the primary data on which all subsequent work should be based. It is well to make sure that the spot chosen for digging the pit is really typical of the soil of the area, and this can be done by making trial tests with a soil auger in

several different places. If the soil is too loose and friable to give a coherent "core" with the auger, or if it is encumbered with stones so that the auger will not penetrate satisfactorily, the spade will have to be used for making the trial tests. The soil should be carefully replaced in all diggings, when they are finished with.

The primary object of interest to the ecologist in the soil profile is the layer or layers in which the *feeding* roots of the plants are situated, and it is these to which his attention should first be directed. Feeding roots can generally be identified by their appearance—fineness of roots, profuseness of branching, presence of root hairs. The general nature of the rooting layers will have been recorded in the profile sketch, and some field tests can now be used.

FIELD TESTS.—Three field tests, designed to give rough information on three important soil factors, are the most satisfactory. These factors are presence and abundance of free calcium carbonate, saturation or degree of unsaturation by basic ions, and degree of acidity.

Calcium Carbonate.—Pouring a few drops of dilute hydrochloric acid on the soil to be tested gives useful information as to the degree in which the soil can be described as calcareous (see p. 89-90, n. 4).[1] Very numerous tests on different layers and on the same layer in different places can be made in a short time and thus the distribution of any free calcium carbonate present rapidly determined—a thing which cannot be done by taking away a few samples of soil for laboratory analysis. If there are comparatively few large particles present at a particular spot the bubbles of gas will be local but vigorously evolved. If there is a much larger number of much smaller particles--of immensely greater effect in neutralising acids because of their much greater aggregate surface—the evolution of gas will be less vigorous but more general. Great local differences may often be observed in carbonate distribution, both from place

[1] The degree of effervescence can be roughly standardised against laboratory determinations with the Collins calcimeter.

to place and especially from the soil surface downwards, owing to progressive leaching of the surface layers. These differences can sometimes be correlated with the rooting layers of different species.

Deficiency of Basic Ions.—Comber's reagent (potassium thiocyanate in alcoholic solution) gives a rapid test of base deficiency or "sourness" in iron-containing soils. The soil solution only takes aluminium and ferric iron into solution when the degree of "base unsaturation" exceeds a certain amount, and only then is red ferric thiocyanate formed with Comber's reagent. The intensity of the red colour measures the degree of this base deficiency with considerable delicacy. If ferrous iron is present it can be converted into the ferric state by the addition of one drop of hydrogen peroxide—a strong oxidising agent—to the solution. If the red colour was obtained before the addition of the H_2O_2 it is now intensified.

It should be noted that since Comber's reagent actually measures the amount of ferric iron brought into solution it is valueless where iron is nearly or quite absent, as in some peaty or humus soils.

Degree of Acidity.—A brief description of the meaning and significance of *p*H value has already been given (p. 176). Accurate determinations of *p*H values are impossible in the field, but a rough idea of soil acidity can be obtained by flooding a little of a particular soil layer with different colour indicators. A common practice is to shake up samples of the soil in a series of test-tubes with distilled water, allow them to settle, and then add appropriate indicators such as those supplied with the B.D.H. capillator set. Settlement may often be encouraged by the addition of a little barium sulphate to the solution.[1] A fairly close approximation to the *p*H value may be had in this way, but there are a considerable number of sources of error, and no reliance can be placed on fine distinctions, such as are indicated by differences of one or two decimal places. It is important to remember that it is not the actual "soil solution"

[1] This procedure is included in the B.D.H. $BaSO_4$ soil testing outfit.

that is being tested, but the solution obtained by mixing the soil with water, which may contain traces of alkali from the glassware used. The salt content of the soil and the proportion of soil to water also affect the result, so that *p*H measurements on water suspensions of soil samples taken in spring and early summer, when nitrate concentration is high, give different *p*H values from similar measurements taken in winter. All working pedologists agree that *p*H determinations on soil are a tricky business, and that accurate and trustworthy results can only be obtained by specialists working in properly equipped laboratories. For these reasons no detailed descriptions are given here of the different methods of *p*H measurement.

Water and Humus Content

There are, however, one or two determinations of important soil constituents that can be made with quite elementary laboratory facilities. These constituents are the water and the organic matter held by the soil. The samples should of course be taken from the layers of soil in which the roots of plants are present. Each sample should be carried in a tin with a tightly fitting lid, and carefully marked for identification.

Water Content.—The amount of water present in the soil should be determined in two fractions. Ten grams of the soil are weighed out, spread out on a sheet of paper in the sun or (in winter) in a dry room, and then weighed again. When the soil no longer loses weight it is "air-dry," and the water lost can be expressed in decigrams, i.e. as a percentage of the weight of the fresh soil. This of course will vary according to recent rainfall or proximity of ground water. The air-dry soil should then be heated in an oven kept at 100° C. and the further loss in weight recorded. This can be expressed as a percentage of the air-dry soil and is reasonably constant for a particular soil.

Loss on Ignition.—The loss in weight when the soil (previously dried at 100° C.) is heated to redness in a crucible or on a sheet of metal, represents the organic content (humus)

together with the "water of constitution" of the clay present, and the carbon dioxide lost by the breaking up of calcium carbonate. In highly calcareous soils therefore the calcium carbonate must be determined separately and the equivalent carbon dioxide (set free when the calcium carbonate breaks up on burning) subtracted from the total loss on burning in order to obtain an approximately correct result for the humus, and in clay soils an allowance must also be made for the loss of their water of constitution, which must also be separately determined from the isolated clay fraction.

It will now be well to summarise the soil characters which are of ecological importance, distinguishing those which can be observed in the field or by the simplest laboratory procedure, marked by an asterisk (*), from those which require investigation by trained workers in well equipped laboratories.

(1) *The general nature and particular characters of the soil profile as seen in a clean vertical section down to the subsoil or parent rock, with particular attention to the root-bearing horizons and those immediately related to them. Colour and appearance of the different horizons should be carefully observed and the whole profile described and sketched.

This inspection and description of the soil profile will convey a great deal of the most important information about the soil in relation to its vegetation.

(2) *The textures, i.e. the proportions of particles of different sizes, of the different horizons can be roughly determined by the proportions in a small sample whose particles sink at different rates when mixed with distilled water.

Accurate measurement of the different fractions is determined by the technique of "mechanical analysis."

(3) *The water content of soil, determined in two stages, is a simple laboratory operation.

(4) The humus content (in the sense defined on p. 183) is determined by the * loss on ignition (a simple laboratory operation).

This loss, however, includes also the loss of carbon dioxide from calcium carbonate and the loss of the "water of constitution" of clay. In "calcareous" soils, and in those which have a considerable clay content, these fractions of the loss on ignition are important and must be determined separately. Their subtraction from the total loss on ignition will give the content in organic matter (humus).

(5) *Carbonate content in more than minimal amount can be very usefully tested by noting the intensity of effervescence caused by dropping dilute hydrochloric acid on the soil (see pp. 89, n. 4, 201). In most cases this carbonate is practically all calcium carbonate.

For accurate quantitative determination the "Collins calcimeter" or a similar method is used.

(6) The degree of "base unsaturation" can be measured by the tint assumed by * Comber's reagent (see pp. 186, 202) in soils where iron is present in more than minimal amounts.

The determination of "total exchangeable bases" (a very important soil character) depends on methods which require the experience of trained soil chemists; and the extraction of particular bases such as calcium, magnesium and potassium, and of "trace elements" (see p. 175) require a properly equipped laboratory.

(7) The determination of nitrates and of ammonia (primarily important soil characters) also require laboratory methods. The Kjeldahl method for total nitrogen often suffices for most purposes.

(8) Anion determination, and total phosphates and sulphates, also require a laboratory.

(9) "Soil reaction" (pH value) may be very roughly determined in the field by the use of * colour indicators, but more accurate quantitative work presents many pitfalls and exact pH determination and interpretation should be left to experts.

(10) Determination of the constitution of the soil atmosphere (e.g. the proportions of free oxygen and carbon dioxide) needs special laboratory methods.

CHAPTER XV

Biotic Factors. Nature and Interaction of Ecological Factors. The Habitat and Succession

BIOTIC FACTORS

THE biotic[1] factors of the habitat are those which depend directly on the action of living organisms on the vegetation. It is obvious at once that here we are involved in a logical difficulty, for the plants included in any community may, as we have seen, have a profound effect upon one another, just as the individuals of a human community have such a mutual effect. In order to get a practicable working definition it would seem we must exclude the mutual effects of members of the community, and apply the conception of biotic factors of the habitat, i.e. of the community habitat, only to the action of organisms which are not regarded as part of the community. But then we are confronted with the question of which organisms are to be regarded as part of the community and which are not. The soil bacteria? Earthworms and other soil animals? Parasitic fungi? The snails and insects that live on the plants or in the soil? The birds that live in the trees and may play an important part either in destroying or in distributing fruits or seeds, or in doing both? Directly we put such questions we begin to realise how closely interwoven is the web of nature, and how artificial our distinctions and classifications in reality are.

The most natural conception that has been suggested is that which regards the whole complex of organisms—both animals and plants—naturally living together as a sociological unit which has been called the *biome*, and whose life must be considered

[1] Greek *βιωτικός*, pertaining to life (*βίος*).

and studied as a whole. The biome will include not only soil algæ, bacteria, and earthworms, not only insects and parasitic fungi, but rabbits, mice and other rodents. In the semi-natural pasture communities, which are maintained in the condition of pasture by grazing, we must include the sheep or cattle which are regularly pastured upon it, and which, as we have seen, are the chief factor which keeps this plant community in equilibrium.

A wider conception still is to include with the biome all the physical and chemical factors of the biome's environment or habitat—those factors which we have considered under the headings of climate and soil—as parts of one physical *system*, which we may call an *ecosystem*, because it is based on the *οἶκος* or home of a particular biome. All the parts of such an ecosystem—organic and inorganic, biome and habitat—may be regarded as interacting factors which, in a mature ecosystem, are in approximate equilibrium: it is through their interactions that the whole system is maintained.

Nevertheless the narrower conception of a plant community still has value if we do not insist on defining its limits too closely. We must content ourselves with the definition of a community already given on p. 30, "any collection of plants growing together which has as a whole a certain individuality." For practical purposes it is necessary to regard separately, and to study separately as a "biotic factor," any collection or group of animals which have marked effects upon a plant community.

The ways in which the effects of such animals can be studied are very various. By acute observation alone the good field naturalist can learn a good deal about them qualitatively, but he is seldom able to tell us exactly how much influence they have, especially where a number of different animals are acting together. To obtain such knowledge it is necessary to make exact experiments, by excluding a given species or type of animal from a portion of the plant community.

Small vertebrates can be kept out of a small plot by enclosing it with a wire netting fence of suitable mesh. One-inch netting

will keep out rabbits, while netting of ¼-inch mesh is necessary to exclude mice, and the wire must in both cases be sunk well into the soil. To exclude rabbits in an area where they are very numerous the buried edge of the netting should be turned outwards at a depth of 6 inches for another 6 inches, so that individuals burrowing just outside the fence with the object of getting into the enclosure will find netting below as well as in front of them. Rabbits will only burrow in this way where there is a severe shortage of food, and thus the vegetation protected by the wires very tempting. The height of the wire above the ground-level should be 3 feet for rabbits, 12 inches for mice and voles. Mice and voles, however, sometimes climb fences of this height. They can be excluded by vertically placed sheet-iron plates or by *covering* the enclosure with ¼-inch wire, which also keeps out birds.

The invertebrates are of course much more difficult to exclude, especially those, such as slugs and snails, which live in or wander through the soil instead of merely traversing its surface. Wire gauze can sometimes be used with advantage for short periods, but this cuts down illumination and prevents the entrance of seeds and fruits into the protected plot. The methods of preventing the access of invertebrates must be left to the ingenuity of workers according to the particular animals to be excluded and the particular conditions of the experiment.[1]

Extensive field work during the past quarter century by animal ecologists, especially the Oxford Bureau of Animal Population, has demonstrated the existence of great cyclical fluctuations in the populations of such small rodents as voles and mice, and since these animals may be very destructive, the marked increases and decreases in their numbers are naturally of great importance in estimating their effects on vegetation.

Animals may work in diverse directions: they may eat and

[1] The student is strongly advised to refer to the records of work that has been done with the help of methods of excluding animals, particularly (**56**) Farrow (II, 1916; III, 1917) for rabbits and (**158, 159**) Watt (1919, 1923) for mice, birds and invertebrates. These papers not only give valuable practical details of methods, but will also enlighten the student on the interest and value of the results that can be reached.

damage vegetation so as to cause, in an extreme case, the replacement of one community by a totally different one, and they may act as pollen or seed distributors, as well as affecting plants in many other ways—altering the soil for instance by manuring, or by loosening or compacting it.

There is good evidence that the regeneration of the grasses and other useful grazing plants of the American cattle ranges in some of the Western States is promoted by the trampling of cattle after the seeds are ripe. It has often been stated that the presence of swine in English oakwoods and beechwoods helped their regeneration from seed, though there is no proof of it. Although the pigs feed on the mast, they are supposed to favour regeneration by trampling some of it into the soil and thus enabling the seeds to germinate; and this may very well be true. It has also been recently suggested that pigs are likely to be of use to the beech by eating various enemies of the seed and seedling, such as mice and slugs. There is abundant evidence that the destruction of carnivorous birds (hawks, jays, etc.) and small animals (stoats, weasels, etc.) by gamekeepers handicaps or destroys the chances of tree regeneration in many of our woods, because the rabbits, mice and voles which are part of their natural prey multiply in their absence and destroy the seeds and seedlings of the trees, especially oak and beech. Thus an interference with the balance of the animal population may alter the relation between one part of it and the dominants of the plant community, and eventually result in the disappearance of the latter.

These are only a few of the cases in which such relations are or may be of first importance, but they serve to illustrate the far-reaching effects that animals may have upon plants. It is much to be desired that field naturalists whose main interest is in animals should co-operate with plant ecologists in the studies necessary to elucidate such relations as those described, and others which must certainly exist, many of them probably still unsuspected.

Nature and Interaction of Ecological Factors

In studying the different factors of the habitat and estimating their combined effect on the vegetation, certain principles must always be borne in mind.

The first principle, already alluded to (p. 131), is that the forces which can actually affect plants are limited in number and nature by the constitution of the plant itself—in the case of the ordinary rooted land plant by those features which are common to all such plants—and also by those peculiar to the species. Apart from "gross" factors, like damage or destruction by wind, frost, fires, grazing animals, insects, parasitic fungi, and the like, when we speak of a "factor" of the habitat such as rainfall, water content of soil, or the kinds and amounts of salts present, we must remember that these can only be effective in a limited number of specific ways—ultimately reducible to water, with its content of free ions capable of absorption by (or otherwise affecting) the roots, free oxygen, CO_2, available light falling on the leaves, evaporating power of the air, and temperature. The term "factor" is in fact used in ecology for any substance, force, or condition affecting the vegetation directly or indirectly in such a way as to differentiate it from other vegetation, and the so-called "factors" have always to be ultimately interpreted in terms of the mechanical, physical and chemical processes directly concerned in the life of the plant.

In regard to the water turnover of the plant, a reduced evaporating power of the air means that the roots will make a smaller demand for water on the soil, so that in a region with constantly humid air the same species can grow on soil which has a lower water supply. Direct evaporation from the soil itself in a humid climate will also, of course, be much less, so that the soil will maintain an adequate water supply with a much lower rainfall than would be necessary in a hot climate. Thus a sandy soil in the West of England, where both rainfall and air humidity are high, will support a more moisture-loving vegetation than the same soil in the Eastern Counties. Again,

in eastern England most soils, owing to the moderately high air humidity, will, with a rainfall of 20 inches, support a more luxuriant vegetation than in a continental climate, where similar soils with the same rainfall might produce only a dry grassland. Similar relations of air and soil moisture may be seen on a smaller scale wherever the physiographical features produce sharp differences of "local climate," as in steep ravines and on exposed ridges.

Replacement of One Ecological Factor by Another.—Such cases as those just mentioned illustrate what has been called the replacement (or compensation) of one factor by another. Thus many of the same species occur on the southern exposures of hills with dry shallow soils in Western and Western-Central Europe as on various different soils and exposures in the drier Mediterranean climate. Here the local physiographic and edaphic factors replace the general climatic factors of the Mediterranean region. Inversely, steep northern exposures (cf. p. 167) and deep ravines in the Mediterranean region often bear a distinctly northern vegetation. Beechwoods in the damp climate of England are practically confined to relatively dry permeable soils (chalk and sand); in the much drier climate of Continental Europe they occur on a greater variety of soils.

Sometimes biotic factors replace climatic ones. On the Swiss Alps in Canton Valais a certain heavily pastured grass and herb community on a dry south exposure showed a strikingly similar vegetation, with the same life forms and the same "aspects," as the Hungarian *puszta*—the heavy pasturing (reinforced by the "local climate" due to south exposure) bringing about a set of conditions similar to those of the continental grassland of Central Hungary. And so in many other instances.

Limiting Factors.—The second principle is what has been called the "law of limiting factors," which is of great importance in ecology. When the co-operation of two or more "factors," e.g. definite quantities of different substances, temperatures within certain limits, a certain intensity of illumina-

tion, etc., are required for the maintenance of any process, then, if one of the "factors" is absent, the process stops whether the others are present or not. Similarly, if the *rapidity* of a process varies with the quantity or degree of several different "factors" acting together, the reduction of any one of them will reduce the rate of the process, even though the others are present in sufficient quantity or degree, or in excess.

Thus the necessary mineral salts may be present in the soil, temperature and light may be favourable; but if water is absent the plant cannot grow, and if minimal amounts are present it can only grow very slowly, as in a desert. Again, if the temperature remains below freezing-point, plants cannot grow, though all the other factors may be present. And as the temperature rises above freezing-point growth will steadily increase up to a certain point if the other factors are maintained in adequate degree. It may, for instance, be checked by the water factor, the water supply in the soil being adequate to maintain the slow growth which can take place at 5° C., but inadequate to the more rapid growth which would take place at 15° C. or 25° C. if sufficient water were available. The rise in temperature will also tend to decrease the water supply in the soil by increased evaporation, both directly through the soil and also through the plants, and this last effect (increase of transpiration) may render the plant unable to cover its water loss by absorption from the soil. And so with the other necessary factors, carbon dioxide, light, and mineral salts capable of absorption by the plant and containing the necessary elements. The factor which is present in so low a quantity or degree that it limits growth or some other life process is called the *limiting factor*.

THE HABITAT AND SUCCESSION.—A final point about the habitat should always be kept in mind—the fact that it may *change* progressively, both along with the vegetation and more or less independently also. This point has already been considered in Chapter IV, where we saw that succession or development of vegetation from a starting-point on bare ground was

normally accompanied by a gradual increase of humus, and that this increase in its turn progressively fitted the ground for different kinds of vegetation until a climax was reached. On all the more favourable soils this climax tends to be determined by climate (climatic climax), and to represent the highest (most complex) type of vegetation that can exist in the general climatic conditions. We have seen in Chapter XIV how humus comes to be of such great importance in "improving" the soil, provided there is a quick "turnover," and thus in helping to provide the most favourable conditions for vegetation. If these favourable conditions are maintained indefinitely the climatic climax will be correspondingly maintained, the ecosystem will be mature.

ACCUMULATION OF MOR.—Other factors may, however, come into play. In a cool humid climate, such as we get on and near the western coasts of the British Islands, the humus does not disintegrate as rapidly as it is formed, and thus tends to accumulate as mor. In the wetter places this results in the formation of peat, and we get bogs and moors instead of forest. This is most marked over soils poor in lime and in mineral bases generally,[1] because the presence of basic ions tends to promote the growth and activity of soil organisms which disintegrate the humus and provide food for the higher plants other than bog and moor plants. But under cool and extremely moist conditions, especially if the soil is badly aerated, raw humus and peat may form even over limestone itself. Here we have good examples of the replacement of factors already described. A cool moist climate, local excess of soil water, poverty in mineral salts, and poor aeration, are all factors tending in one direction, and may to a considerable extent replace one another.

LEACHING.—Another factor tending to alter the habitat in the same direction, and having a considerable effect in the British Isles, is the leaching or washing out of soluble mineral salts. Different salts are soluble in very various degrees. Sodium chloride and the other haloid salts left in maritime soils wash

[1] It is, however, held by some workers that a preponderance of potassium and sodium over magnesium and calcium in the water favours the growth of moor and moss plants as well as a corresponding aquatic vegetation.

out the most readily, and thus alter the habitat presented by these soils when they are no longer supplied with fresh salt. Of the salts present in ordinary soils calcium carbonate is most readily leached out by water containing much carbon dioxide, while magnesium and potassium salts dissolve much less quickly. The impoverishment of the surface layers of soil in calcium carbonate and, to a less degree, in other bases, will lead to "acid conditions" and to the establishment of acid-tolerant plants, and may gradually change the whole character of the vegetation. It is believed that much of our semi-natural vegetation has been, and is being, steadily altered in this way. In wet regions leaching will clearly assist peat formation, in drier ones it will slow down the turnover of humus and thus tend to the accumulation of mor, for instance on a forest floor; and this may help, along with other factors, to prevent the regeneration of the forest, or lead to the replacement of one species of dominant tree by another.

Effect of the Nature of Litter.—Another factor leading to the formation of mor is the nature of the plant debris from which the humus is derived. The leaves of woodland trees, for instance, differ very considerably in their resistance to the processes of decay and this is broadly correlated with their acidity. Conifer needles, particularly, are very resistant, so that the litter they form tends to accumulate and decomposes very slowly. Spruce litter has a *p*H value of 3·8, pine of 4·5, and both tend to form mor. This fact has an important bearing on the great plantations of conifers now being made by the Forestry Commission. Pure plantations of these trees tend to change the type of humus from mull to mor, increasing the acidity of the surface soil, promoting leaching and the degradation of soils from the Brown Earth to the Podsol type. Most deciduous trees form litter which decays much more quickly and humus which is less acid. Beech litter, with a *p*H value of 6·6, is more resistant to decay than oak litter, and on a sandy soil, poor in bases, easily develops mor, though on a loam of high base status it forms a good mull. The tree regenerates well on such a loam,

but often fails to do so where the litter has formed mor on a sandy soil poor in bases.

FLUSHES.—Where the surface soil is constantly supplied with fresh bases these changes will not occur. The "flushes," as they are called, often seen in grassland and in woodland on sloping ground, are areas irrigated by water from springs or from the run-off of rainfall on the ground above. If these waters contain mineral salts as well as free oxygen in solution, the flush will bear a distinctive vegetation of various grasses, herbs, etc., often fresh green in colour in the midst of a brownish acid-tolerant vegetation of the general hillside. In other cases an "acid flush," with acid-tolerant plants in the midst of a vegetation of plants growing only where they can obtain a good supply of bases, may be formed by water draining from a moss or moor.

PART V

Ecological Work in Schools

CHAPTER XVI

Ecology and "Nature Study"

THE author is convinced of the great educational value of ecology in schools, and it is hoped that the foregoing chapters will enable masters and mistresses to get some clear idea of the possibilities of the subject and of the ways in which it can be approached and developed in the garden and field. It is unnecessary to say that this book is not intended—is indeed obviously quite unsuitable—as a school class-book.[1] Much of the work suggested could not possibly be undertaken by school classes, and the book is written for the adult mind, though it is hoped that most of it at least will be intelligible to those who have had no very detailed training in botany.

This chapter and the next contain specific suggestions to teachers—rather different in scope from those contained in *Plant Ecology and the School* but with the same basic ideas—as to the ways in which ecology can be used in schools. Opportunities for such work vary widely between different schools.

[1] *Plant Ecology and the School* (Geo. Allen & Unwin Ltd., price 6s.), by A. G. Tansley and E. Price Evans, has been written in conjunction with a secondary schoolmaster and is addressed directly to teachers as a first introduction to the subject, especially in connexion with Geography.

In a city school with no school garden it is practically impossible to carry on any systematic work in the subject. The most that could be done would be to try to arouse some interest in vegetation on country excursions, but without some previous acquaintance with the species of plants even this would probably not be very profitable or successful. Botany, of course, can be taught—after a fashion—in a city school, but scarcely ecology, which must depend on first-hand acquaintance with plants in the field and garden.

In a school placed in a country town or in the countryside itself the case is quite different, but any considerable development of the subject must depend on two other factors—the whole-hearted sympathy of the headmaster or mistress and the aptitude and enthusiasm for such work of the actual teacher. In the absence of the first it would be difficult or impossible to find the necessary time and opportunities, and without the second it is most unlikely that the pupils would ever become sufficiently interested to make the thing worth while. The suggestions and hints which follow can therefore be made full use of only by those who are fortunately situated in these respects.

At the outset it must be borne in mind that ecology, in the wide sense explained in Chapter I—and it is, of course, in this sense that its school value is to be considered—is essentially *a way of looking at plants. It should never be divorced in teaching from the actual study of the plants themselves, of their structure, development and functions.* But the relative importance of the various characters presented by plants can be interpreted from the ecological point of view. In other words, the features of plants can be looked upon as of importance in relation to their actual life in the field as members of plant communities rather than from other points of view.

"NATURE STUDY"—THE FOUNDATION OF ECOLOGY.—Ecology is nature study *par excellence*, and although the work in the lower forms of many secondary schools that is called "nature study" is not exactly ecology, it can very well be used to form a good foundation. In a school where the opportunities exist

and the conditions are favourable, it is most desirable to begin early, and to continue throughout the school course, open-air work in which ecology can play its part.

There is no better starting-point than the germination of the seed and the structure and growth of seedlings. This work can be adapted to any age, and the whole of it can be followed and observed by the children, who can grow the seedlings of different plants for themselves in pots and boxes, and in the garden if there is one available. They can learn the origin and history of the different structures produced, and, by the simplest experiments, some, if not all, of the necessary conditions for germination and subsequent growth.[1] They can see how widely the seeds and seedlings of different kinds of plants differ from one another, and yet that there is a general plan of structure common to them all.

Here may be introduced some early lessons on soil, even simpler and more elementary than the work described in Russell's *Lessons on Soil*, if the children are too young for that. It is most desirable to keep the study of the soil in the closest relation to the study of the plant from the very beginning. The differences between garden soil and natural soils can be illustrated by actual examples from the neighbourhood. A first study of seedlings and soil might very well occupy one term. Let us say it is the second winter term, a very suitable time for such work.

If the course begins in the autumn a start may be made with fruits and seeds. As many as possible should be collected from every source, and the different plans of structure examined and drawn. When possible, the development of fruit from the flower should be followed: it does not matter if no study has yet been

[1] The quantitative estimation of the water present in the seed, the minimal temperature for germination and growth, and the oxygen supply necessary, are of course suitable only for older pupils. But the necessity of these factors can be clearly established by quite young children with a little ingenuity on the part of the teacher. "The little baby plant sends out its tiny roots to search for water," and all such sentimentality should be rigorously avoided. It is alien from science and brings the subject into contempt with natural healthy-minded children

made of the flower itself. The swelling or change of the carpels can quite well be taken as a starting-point. The work on fruits and seeds may be continued after Christmas, and the germination of seeds only begun in February or March, at first indoors, and continued after Easter, when seedlings are springing up vigorously everywhere.

In the summer term it will be natural to tackle older plants and flowers. The particular work must now depend very much on the age of the pupils and on the particular school and its opportunities. For instance, if there are facilities for indoor laboratory work, and neither garden nor field work can be made a feature, simple experiments on growth, perhaps also on transpiration and photosynthesis may be carried out, and at the same time different types of life form (see Chapter V) examined and compared. To this the structure and functions of the flower and the comparison of a *limited number* of different types of flower may be added. These topics will probably amply fill the summer term.

If, on the other hand, the school garden is a feature of the school, and the children are allowed to work in it, they can begin to get an invaluable first-hand acquaintance with many things: cultivation of the soil; growth of different life forms from seed, from rootstocks, from corms or bulbs; effect of different kinds of weather on different plants; weeds and their life forms, e.g. the difference between the comparatively harmless annual weeds, like shepherd's purse and groundsel, which in moist weather can easily be pulled up with the finger and thumb, and the pestilent weeds with deep-seated, quickly growing rhizomes or suboles, like field bindweed, twitch and the like. All these things afford ample material for drawing in the classroom, and thus fixing in the memory.

It is, perhaps, unnecessary to say that the ideal of a school garden for teaching botany is not a "tidy" garden devoted to well-kept flowers and crops of vegetables, but an outdoor working laboratory for studying the growth of different kinds of plants and the conditions under which they succeed or fail.

Certain beds may be kept for the production of flowers and vegetables, and in these the lessons learned in the "working" beds may be applied. But in the latter the children should by no means be forbidden, they should be encouraged, to dig up seedlings and older plants "to see how they are getting on," to look at the nature and development of the underground parts, the depth at which these grow, and so on. It should be a point of honour to know exactly what the underground parts of every kind of plant grown and of every weed are like, and the kinds of plants grown should be chosen largely to illustrate different life forms. They should be sufficient in number for this purpose, but not too many.

Finally, if half-day excursions to the open country are possible—say once a week—these may be made the pivot of the term's work. Following on the general knowledge of seedlings acquired during the spring, one of the first excursions may be devoted to marking with stakes (inconspicuous if the place is frequented) or otherwise, sets of seedlings that are met with on waysides, hedgebanks, the edges of woods, and in arable fields, with a view to observing them week by week and noting what happens to them. Some will die and disappear from causes not easy to discover, some will be smothered by the growth of neighbouring plants, or will starve each other of light, grow up long and spindly, and finally die. Some may be attacked and crippled or destroyed by minute insects or by parasitic fungi, others trampled down or eaten off by browsing or nibbling animals. Others, again, may dry up from want of soil water. But some will grow into adult plants, and interest will be aroused and maintained as to what plants they will grow into. These can be watched week by week and their progress noted, until the time comes when the plants can be identified.

During the first few weeks the discovery of seedlings that can be marked, and the observations upon them, will occupy a large part of the time available. Where there is an abundant crop, specimens should be carefully dug up and taken back to school in tin boxes, to be drawn to scale, the earth having been

carefully washed from their roots; and so from week to week if the seedlings have grown enough. As time goes on, so many will have disappeared, and the ones that remain will be so well known, that less and less time will be required for following their progress.

Meanwhile other matters can be attended to. A certain number of perennial plants can be chosen for study. The particular species chosen must of course depend on what grows in the neighbourhood. They should not be too numerous (perhaps half a dozen), and they should all be common plants, so far as possible characteristic of different communities, e.g. a woodland plant like dog's mercury, stitchwort, or wood violet, a heath plant like the ling itself, a wayside plant like silverweed or a species of plantain, one or two pasture plants, including a dominant grass, and so on. To these may be added two or three annuals, preferably those whose development has been followed from the seedling.

In a mainly agricultural region, where most of the land is under the plough, at least half the plants may be chosen from among arable weeds, and the balance from hedgebank and wayside plants. But if any areas of comparatively natural vegetation exist in the neighbourhood, such as heath, common or down, then dominant or characteristic plants from these should certainly be included in the list.

Everything possible should be ascertained about the species chosen, including as many as may be of the following points: life form, i.e. mode of perennation, depth at which the roots are mainly developed, general structure of shoot system, vegetative propagation; any soil preferences or other habitat preferences that may be observed, time of coming into flower, duration of flower, structure of flower, mode of pollination,[1] whether seed is set and ripened, and if so how much; relations

[1] Direct observation of insects visiting the flowers and their behaviour will often show the method of cross pollination. The simple experiment of tying a muslin bag over the flowers will show whether large insects are necessary, but small insects (e.g. Thrips) can crawl through most muslins. The muslin may also, in a wet season, interfere with evaporation sufficiently to cause the flowers to rot.

to other plants (competition, etc.). This will be a sufficient programme for the summer term, and if the children are very young, it will have to be considerably simplified, for instance, by cutting down the number of species chosen for study, and also the points studied. But the *kind* of work required is important, for the kind described draws out and trains the powers of observation, raises all sorts of interesting questions, some of which can be answered at once, while others may be answered in later years. At the same time such work is undoubtedly the best foundation for the future. It need not be said that more work than can be properly carried out should not be undertaken.

It may again be emphasised that the suggested work in the laboratory, garden and field are intended as *alternatives*. If it should happen that any of the three would be possible, the garden is probably to be preferred as the pivot of the work during the first year, and, after the garden, the field is probably to be preferred to the laboratory from our point of view, because either garden or field brings the children from the outset into touch with plants as they grow. Either garden or field work should be supplemented by classroom work for drawing, recording observations in permanent form, and discussing results. So far as may be, both individual emulation and also co-operation should be used to stimulate work, and the putting of questions to nature should go hand in hand with observation.

The age at which nature study work is begun must, of course, determine the fullness with which such a programme as that suggested for the first year could be carried out. If the average age of the pupils is eight or nine, it would clearly have to be restricted and simplified; with bright children of ten or eleven it might be followed fairly closely. In the former case a second year's work might follow the lines of the first with fuller material, or the field or laboratory might be used instead of the garden. In the latter case fresh material may be introduced. For instance, trees instead of herbs could be taken as the main subject of the second year's work. The fruits of available trees, especially the

commoner British ones—oak, beech, ash, birch, pine, with sycamore and any others accessible—could be studied in the autumn, and the opportunity of early autumn walks taken to observe the natural dispersal (or non-dispersal[1]) of those fruits (notably oak, beech and sycamore) which are shed at that time. This work could be supplemented by observation of the method of leaf fall and of the winter condition of the trees—the general shape of the different kinds, the form, colour and protection of the twigs and winter buds, the bark of the trunk, etc. The children could be asked to draw some of the kinds of tree from memory at the beginning or early in the course, and the results would at once reveal how far they had already observed their forms and could express them on paper. The attempts would serve as good starting-points for more deliberate observation.

In the spring, seeds which had been collected and kept (perhaps under different conditions, e.g. moist and dry, well aerated and closely packed) could be put to germinate and the results observed. The process of germination and growth of the different seedlings could then be followed. Afterwards the best seedlings could be planted out in the garden.

In the late spring and summer the leafing of the different trees should be observed, the shade they cast and the shade the seedlings and young trees can endure compared. The structure of the flowers and their mode of pollination should be looked into.

If woods are accessible, some of the ground species which grow in shade or half-shade can be taken up for study on the lines suggested above, in addition to the species chosen for the first year's work. In this way the beginnings of a study of woodlands can be made.

[1] Do the shed fruits of these trees really contain fertile seed? Beech mast, for instance, often does not. Do they get far from the parent tree? If so, how?

CHAPTER XVII

Development of Ecological Work

It is probable that two years of nature study devoted, or mainly devoted, to plants are enough. In public education the pupil who leaves the primary or elementary school at eleven and continues to learn science at a central or a secondary school is taught only specialised science, so that he may cease to learn any biology at that early age.[1] In the author's view it is educationally bad to stop the teaching of biology in this way. While admitting that chemistry and physics are basic sciences and that they are naturally of most use in industry, he is strongly of opinion that the biological interests that have been aroused by nature study should be maintained throughout the school course. Biology, in some form, should be regarded as of primary importance, if only because we ourselves happen to be living beings. The author thinks that at least one teaching period a week should be devoted to some form of biology throughout the school years, and that this should be reinforced by the establishment in country schools of a Field Club or Natural History Society, and by the encouragement of voluntary work at some branch of the subject.

It is by no means necessary, of course, that ecology should be the pivot on which this "continuation biology" should turn. In city schools it cannot be; and besides, there are other ways of treating biology, particularly those leading up directly to its bearing on human life, which have the most serious claims. On the other hand, there are many country schools where ecology is certainly suitable, and if it is properly taught it must stand very high in educational value. We may now, therefore,

[1] Unless "general science," including some form of biology, is taught.

consider the lines along which it may be developed, either as a regular school subject, or as voluntary work of the pupils and teacher. The most desirable thing is that it should be partly one and partly the other, and the adjustment of the two spheres should not be beyond the powers of an enthusiastic teacher, supported by the sympathy of the head of the school. Possible lines of work will be outlined in quite general terms, since it is clear that the detailed adaptation to special circumstances must be made by the teacher.

The earlier nature study on the lines suggested will have taught the facts of the life history of a limited number of species pretty thoroughly, and should have laid the foundation of the habit of looking at plants in the right way. The work may now be developed either on intensive or on extensive lines. The immediate advantage of intensive work is that it does not require a wide and accurate knowledge of the flora. If the work is confined to small plots of ground, all the species met with will soon be well known and easily recognised at all stages of growth, and a fairly exhaustive knowledge of their life histories obtained. This sort of work is very attractive to some minds, and it is excellent training in thoroughness and careful attention to detail. But it does not appeal to all, and a more superficial acquaintance with a much wider range of species and of vegetation, which may be accurate enough as far as it goes, is also very good training, though better for rather older minds. Extensive work is only practicable, of course, when there is freedom to move about the countryside. The ideal thing, no doubt, is to begin with the sort of work suggested as nature study, to go on with intensive quantitative work, and later to widen the range by extensive observation.[1] This course may very well be possible in the case of a few of the keenest pupils at a school where ecological work is an established feature of the curriculum.

[1] The thesis laid down in Chapter VIII, that extensive survey is the best preparation for intensive work, applies to adults freshly approaching ecology, not to the training of children.

THE USE OF THE QUADRAT.—The different uses of quadrats in the study of vegetation have been described in Chapter X. For intensive work at schools the quadrat is invaluable, and particularly the permanent or semi-permanent quadrat which is charted or listed at intervals.

GARDEN QUADRATS.—If there is a school garden, a certain number of quadrats on bare soil should be laid out and made permanent with corner pegs and durable laths or rods marked in small divisions (decimetres[1] or 6-inch intervals). If there are marked differences of soil in the garden, or one part is always wetter than another, or some parts are shaded and others exposed, one or more quadrats should be laid out in each. It is best to lay out the permanent quadrats in the winter when the soil is quite bare. Access to each quadrat must be provided for. It has to be remembered that approach must be possible in all states of the soil. A quadrat cannot be accurately charted unless the observer can get his eyes close to every part of the surface, so that it becomes necessary to kneel or even lie beside it. Strips of waterproof should be provided, or clothes will be likely to be made very dirty, especially if the soil is at all heavy.

The garden quadrats should be first charted as soon as the first crop of seedlings appears, and thereafter at fortnightly or monthly intervals throughout the summer term, and again immediately after the summer holidays. The seedlings will, of course, be mainly "weed" seedlings, though some of the more easily dispersed garden plants may appear. It will be impossible at first to distinguish the seedlings of different plants, though different types of cotyledons will be noticed at once. Consequently symbols must be decided upon for the different unknown seedlings, preferably crosses, dots, circles, etc., and these must be at once recorded, with a short description of each, on the space left on the chart card (see p. 125). Later, fresh symbols will have to be added as new seedlings appear.

[1] If any considerable number of the pupils are likely to specialise in science, it is an advantage to use the metric system from the beginning. The boundary laths of the square metre may then be marked permanently in decimetres (red) and centimetres (black) with good oil paint.

Attention should be paid to the remarks on p. 127 about the size of the symbol being proportionate on the chart to the space occupied by the plant on the ground. If the seedlings come up very numerous and thick it will be impossible to chart the whole quadrat properly on the 1 : 10 scale. In that case a part of the quadrat only (say one quarter or even less) should be charted, strings or tapes being run to make the two internal boundaries of the portion to be charted. A careful note must be made of the scale actually employed and of the part charted. Always use the same size of blank chart (a square decimetre is the best), and see that the symbols are not unduly crowded by taking care to chart an area of suitable size. If only a portion of the square metre can be charted at first, yet later on, when many of the seedlings have disappeared owing to various causes, it is probable that the whole square metre can be charted on the 1 : 10 scale.

As the seedlings grow the species to which they belong will gradually be identified, and in this way a very full knowledge of the garden weeds, their rate and mode of development, is acquired. As soon as the seedlings denoted by a certain symbol on the first charts are identified as a particular species the initial letter (see p. 120) of its name should be substituted for the symbol of the earlier charts, and the new symbol (letter) with the name it denotes written in the space below the chart.

Every chart must be designated by a letter or number or both[1] and carefully dated. The charting should be done very neatly in pencil, and inked in as soon as possible after completion. All these charts must be carefully kept in a safe place, always available for reference. Comparison of the successive charts of the different quadrats from year to year will furnish most instructive data for drawing conclusions of various kinds.

It will certainly be found that the different quadrats will show at least somewhat different plant populations, though many of

[1] It is convenient to give every permanent quadrat in the garden a letter, A, B, C, etc., and add a number to the letter on each fortnightly (or monthly) chart. Thus the second chart of the third quadrat will be C2, etc.

them will have several species in common. The differences will partly depend on what seeds were in the soil to start with; they may be related to habitat (soil differences, water, shade, etc.), they may be related to proximity of seed parents, or they may be a matter of chance. All these possible causes of difference will furnish useful points for consideration and further study. Besides the first colonisation, there will be a succession of plants from year to year on the same quadrat. Some species will remain for a long time, others will be very transitory. It is, of course, very much to be desired that all the permanent quadrats should remain undisturbed for as many years as possible. The longer they are left the more instructive they will become. No plants should be pulled up or disturbed in any way. The dead ones must be left to rot where they die. If a quadrat should become the centre of distribution of a pestilent weed which spreads by underground rhizomes or suboles, it may be isolated by digging a narrow deep trench round it, but not so close as to drain the soil of the quadrat.

The interest of permanent quadrat work is very great, and no one who has once become fairly fascinated will readily abandon it. The detailed knowledge of the behaviour of seedlings and older plants that is acquired, and most easily acquired, even in one season's work, is astonishing. The effort to chart the quadrat accurately directs the attention towards and fixes it upon details that would very likely be missed altogether with ordinary observation, while the re-observation of the same individual plants at definite intervals gives an extraordinarily close picture of their growth and development. Root systems cannot, of course, be studied on the permanent quadrat itself because the plants must not be disturbed, but examples of the same species from other parts of the garden can be dug up for examination. If desired, the record furnished by the succession of quadrat charts can be completed by series of drawings of the different species represented.

Garden quadrats can, of course, be used for all kinds of purposes besides tracing the succession of plants on the per-

manent quadrats. For instance, experimental quadrats can be laid out, and various experiments tried upon them—over-watering, protection from rain, various kinds and degrees of shading, various kinds of manuring, determination of the seeds introduced with stable manure or other dung, and so on. If the method of teaching by means of the study of quadrats is found to be successful enough to warrant a wider application—and if the facilities described can be obtained and the necessary time devoted this will probably be the case—experiments of the kind indicated will readily suggest themselves to the experimentally minded teacher.

Field Quadrats and Transects.—It will seldom be possible in school work to make such extensive use of permanent quadrats in the field as in the garden, if only because spots in which they can be usefully laid out with no danger of disturbance are often hard to find. An established plant community may show little change from year to year, so that a quadrat, unless it is treated experimentally, will teach little but its original structure. Charting a temporary quadrat, however, is one of the best ways of finding out the detailed structure at any spot of a close complex community, such, for instance, as old-established grassland, because every square inch of ground must be examined. Temporary quadrats of smaller size and in greater number are also very useful for listing with a view to ascertaining the occurrence and frequency of different species.

On bare or partially bare soil which is being colonised, or wherever change is going on, permanent or semi-permanent quadrats are useful for studying succession, if they are reasonably secure from disturbance. Permission from a friendly land-owner and the goodwill of keepers, shepherds, etc., is very desirable and may be indispensable. The outlines of procedure are just the same as in the garden. The quadrat should be charted at regular intervals, though these need not be so short, because growth and change is rarely so rapid as in the garden. Three charts during the season (say April, June and September) are generally enough, even early in succession and when there

are marked seasonal aspects. Often one chart in the year will be enough. But what is necessary in any given case can only be determined on the spot.

Line transects and belt transects (pp. 121–124) are particularly useful at right angles to the direction of the zones in any zoned vegetation. The advantage of a line transect is the rapidity with which it can be made. Thus more than one line transect, if not too long, can easily be made by a party on an afternoon's walk, provided the species present are known beforehand. A long transect can be split up into sections and different members can work at different sections simultaneously (two at each).

Extensive Work in the Field.—For this, of course, a knowledge of the flora is indispensable. Pupils will soon learn the names of the limited number of species that will be met with as weeds in a garden or on a given small set of quadrats in the field, but the two or three hundred species, of flowering plants alone, which will be commonly met with in the various communities of even a limited area of countryside, are quite a different matter. It is doubtful whether it would be possible or desirable to insist on such knowledge being obtained by all pupils, even in a school where field botany could be made a special feature of the school work. A few would acquire it willingly, but not the majority, and it is more than doubtful if any good purpose would be served by compulsory acquisition of such knowledge. It will therefore be necessary to make any thorough extensive work that may be undertaken, voluntary work, carried out by a few of the older and keener pupils.

It is nevertheless very desirable that all school botany should include a certain serious knowledge of the differences between species,[1] though the number of species may be quite limited. This kind of knowledge is probably best and most easily acquired at the outset by the necessity of identifying the plants which appear on garden or field quadrats or field stations under observation, because so much more interest is centred on them

[1] A good flora and illustrations should always be available for reference.

than on specimens brought in from outside. But some regular lessons on the differences between species should also be given, and the empirical knowledge already acquired on the quadrats will be most useful here. It cannot be too strongly insisted that such lessons should begin with the *smaller differences*, i.e. those between *allied species of one genus*, and *not* with families and classes. The plantains, the buttercups and the speedwells are excellent genera on which to make a start; and only when a firm grip has been obtained on the nature of specific differences should the conceptions of genera, families, and larger groups be taken in hand. This depends on the fact that species (or many of them) are real natural entities, while the higher taxonomic groups merely represent the human effort to classify the species. If taxonomy is taught "from the top," for instance by beginning with the characters of classes or families, it often happens that no real first-hand knowledge of species, i.e. of the things actually classified, is ever obtained; and no one can have any sound or useful knowledge of systematic botany who does not know species. From the educational point of view, the *number* of species he knows or is able to put into genera or families at any given moment is of relatively minor importance. Once he has got a firm grip of the *kind* of difference that separates species and the habit of looking at these, he can always easily extend his taxonomic knowledge at will. If he never gets this grip and habit, he can never acquire any sound taxonomic knowledge at all. Furthermore, acquirement of the power of discriminating small differences in natural objects is a very valuable mental training, of use in every occupation and department of life.

It is therefore suggested, on all grounds, that the identification and discrimination of species should form a recognised part of the teaching in botany immediately following and continuing the "nature study" period.[1] The species chosen should

[1] There are few, if any, school floras really good as an aid to this work. Artificial dichotomous keys are not to be recommended, even if they are efficient. They give false notions of actual differences, and emphasise the

be partly groups of allied species belonging to single genera (*Veronica*, *Lamium*, *Ranunculus*, *Stellaria*, *Cerastium*, *Plantago*, *Poa*, etc.), and partly dominants and other common species of easily accessible plant communities. After a year or two at this kind of work, with frequent opportunities of seeing the species in the field, a good acquaintance with from fifty to a hundred species of flowering plants should be easily obtained, and those pupils who have a natural taste for this part of the subject will rapidly widen their knowledge as time goes on.

From the beginning (in the nature study course) different "life forms" i.e. the vegetative structure of the whole plant, will have been distinguished, and attention directed to the habitats, i.e. the kinds of places in which the species are habitually found. Of course, one life form is by no means confined exclusively to one habitat. But certain correspondences will be noted: for instance, the tall slender shoots of reedswamp plants, the prevalence of long underground shoots in all kinds of loose or soft soil, whether woodland humus, the wet soil of marshes and watersides, or in the perennial weeds of loose garden soil; the dominance of annuals in ploughland, garden beds, and on bare soil generally; of plants, like the turf-forming grasses, which branch freely from buds close to the surface (either just below or just above) in pastures and on lawns.

With so much knowledge of species and life forms the study of a plant community in the field may be taken up. What the particular community will be must depend mainly on what is readily accessible. A heath or any kind of common land often best fulfils the necessary conditions; woodlands less often, because they are usually private property and are often preserved for game, though they afford one of the widest and most interesting fields of work. Marsh and water vegetation is very interesting, but regular study of it presents difficulties and

process of identification at the expense of a real knowledge of specific characters. The best floras are unsuitable for beginners. It is suggested that the making of synopses from the actual plants, at first of the species of a genus where several species can be obtained, later of the genera of a family, would be a valuable class exercise.

inconveniences. A seaside school within reach of sand dunes and salt marshes has an unrivalled field of work.

The methods of work on a plant community in the field may be selected from those described in earlier chapters. Here we need only summarise the principal things that should be done, beginning with those that naturally come first. But it is not necessary, of course, to take them exactly in this order, nor to complete one before beginning another.

1. List of species, as complete as possible, and identification of those not already known.
2. Preliminary attempt to determine the minor plant communities (consociations or societies) present.
3. Vegetation map or chart on a scale suitable to the area and type of vegetation (Chapter IX). This is only worth making if the distribution can be correlated with habitat conditions (of whatever kind), or there is an obvious general invasion or succession proceeding. If the vegetation is substantially uniform over the whole area (apart of course from local variations not obviously correlated with habitat), there is little point in making a general map. In a diversified agricultural region making crop maps based on the 6-inch Ordnance Survey maps is an interesting and instructive exercise. A series of crop maps, one for each year, will give interesting information on the different systems of agricultural treatment.
4. Quadrat and transect charts. These may be used for getting a closer idea of the structure of the vegetation, but are not always worth while in uniform and stable vegetation. The teacher must use his judgment. If, however, the vegetation is zoned, or succession is clearly proceeding, either generally or locally, transects or quadrats, or both, should certainly be laid down, and the changes followed in successive years.

5. Studies of habitat factors (see Chapters XIII–XV), including for instance regular grazing or rabbit attack.
6. Special studies on various questions that may arise in the course of the earlier work, e.g. problems connected with seed dispersal, or effect of fires (regeneration or replacement by other vegetation, etc.).

Work of the kind suggested, carried out on a favourable community and continued for some years, would not only have great educational value, but would also almost certainly contribute sufficiently to our knowledge of ecology to be well worth publication. A tradition of genuine observation of nature will be gradually established in the school, with literally incalculable benefit to many of the pupils, and benefit also to the progress of ecology itself.

If no such detailed study of a particular community is possible, something can be done on half-day excursions to different communities, e.g. different types of common, down, woodland, mountainside, fen, or sea shore. Though the knowledge obtained will necessarily be more superficial, the work should *not* be confined to making lists of the species encountered. It will, of course, entail a wider knowledge of species, and if the foundations of species discrimination have been well laid, will arouse considerable interest. The different sets of life forms should be noted, and characteristic specimens and soil samples brought home. Line transects and list quadrats can be made in a short time, and successive visits will eventually amass considerable knowledge of the various communities and their successions and habitats. Even if regular work on a single community is possible, it is good to intersperse it with visits of this sort to other types of vegetation.

THE GROUPS OF NON-VASCULAR PLANTS.—In what has been said above no specific reference has been made to the lower plants—mosses, liverworts, lichens, algæ and fungi—which are often important elements in communities dominated by vascular

plants, and not seldom form well-marked minor communities of their own. The lower plants are, in fact, too often neglected by working ecologists, usually from ignorance of their species, though there is, in recent years, considerable improvement in this respect. It is no light task to obtain even a moderate working knowledge of all these groups. But something can and should be done by the teacher who undertakes to conduct ecological work in the field. A beginning may be made with the commonest mosses and lichens, the names of which can be ascertained without too much labour with the help of the standard handbooks on these groups (see list, p. 237). Gradually the forms most commonly met with in the plant communities taken up for study will become well known to teachers and pupils. The British specialists on these groups will always give ready and courteous help to serious students in naming the rarer and more difficult species. As time goes on it is very likely that some of the older pupils will come to take special interest in different groups, and may become "authorities" to whom unknown specimens will be brought.

The non-vascular plants should certainly not be neglected altogether, not only on account of their intrinsic interest, but because they are often important pioneers in succession. Certain species, also, are of diagnostic value as constant members of particular communities of higher plants.

Relation of Ecology to Other Botanical Work in Schools.—It will have become clear from what has been said, that, where the opportunities exist, ecology in the widest sense, including ecological work in the garden (rather than "gardening" in the ordinary meaning), may well be made the pivot of a regular botanical training. As was stated at the outset (Chapter I), ecology in the wide sense is a means of approach to a large part, and that the most important part, from the point of view of the school, of the science of plants.

The most thoroughgoing way in which this means of approach can be employed is to use the plants of some neighbouring community or communities, as has actually been done

in a boys' school in the North of England (Price Evans, 1920)[1], as the basis of practically the whole of the school work in botany. If these wild plants are supplemented by certain almost indispensable types, such as the broad bean, the French bean, the gourd or marrow, some common cereal such as maize or wheat, and perhaps the castor-oil plant, which can very easily be grown in the garden, hardly any material from outside will be required. The elements of morphology and of plant anatomy can be learned, and the simpler physiological work commonly done in schools can be well carried out on the plants thus available. If the teaching is based on the development, structure, growth and maintenance of the plant as a living being, not only isolated, but as it actually lives in nature, the ecological work proper will bear the right relation to the work necessarily carried on indoors, whichever preponderates in point of time spent on it; and only in this way, the author believes, can plants be used as they should be used in schools, as a means of acquiring a real first-hand knowledge of one of the most important elements of the environment of man.

[1] See *Plant Ecology and the School*, pp. 29, 30, 51-3

Classified List of Books and Papers

BOOKS

The following is a selection of books most useful to the ecological student.

General.

Tansley, A. G., The British Islands and their Vegetation. (Camb. Univ. Press.) The standard reference book on British Vegetation.

Salisbury, E. J., The Reproductive Capacity of Plants. (Geo. Bell & Sons, Ltd.)

Life Forms.

Raunkiaer, C., Plant Life Forms. (Clarendon Press.) Contains descriptions and drawings of typical life forms, many of them British.

Floras.

Clapham, A. R., Tutin, T. G., and Warburg, E. F., Flora of the British Isles (Camb. Univ. Press). This is a full modern British Flora and is without a rival. There are, however, a considerable number of *errata*, a list of which can be obtained from the publishers.

Druce, G. C., A Botanist's Pocket Book. (Geo. Bell & Sons, Ltd.) This is the most useful *field* flora with brief diagnoses of species of vascular plants.

Lower Plants.

Dixon, H. N., The Student's Handbook of British Mosses (Sumfield, Eastbourne).

Macvicar, S. M., The Student's Handbook of British Hepatics (Sumfield, Eastbourne).
The standard works with descriptions and illustrations of every British species.

Carleton Rea, British Basidiomycetes (Camb. Univ. Press).

Ramsbottom, J., Handbook of the Larger Fungi. (Longmans and Oxford Univ. Press). Both standard works, the former fully illustrated, the latter including Ascomycetes.

Practical Handbooks for Fieldwork.

McLean, R. C., and Cook, Ivimey, Practical Field Ecology. (Geo. Allen & Unwin, Ltd.)

Soil.

Robinson, G. W., Soils: their origin, constitution and classification. (Thos. Murby & Co.) The standard English work on pedology.

Robinson, G. W., Mother Earth: letters on soil. (Thos. Murby & Co.) A more popular and very instructive book.

Clarke, G. R., The Study of the Soil in the Field. (Clarendon Press.) A practical book from the pedologist's standpoint.

Soil Analysis.

Piper, C. S., Soil and Plant Analysis. (Univ. of Adelaide.) A standard laboratory manual giving full details of exact modern methods.

For School Use.

Tansley, A. G., and Price Evans, E., Plant Ecology and the School. (Geo. Allen & Unwin, Ltd.) A guide to ecological work in schools intended primarily for teachers.

Suitable for Direct Use in Lower Forms.

Praeger, R. Lloyd, Weeds: Simple Lessons for Children. (Camb. Univ. Press, 1913.)

Russell, E. J., Lessons on Soil. (Camb. Univ. Press.)

Gregson, M. M., The Story of our Trees. (Camb. Univ. Press, 1912.)

PAPERS ON BRITISH AND IRISH VEGETATION 1900–1944

(A) Reconnaissance and Primary Survey

(including the original series of Primary Surveys with Coloured Vegetation Maps)

Scotland

(1) Hardy, Marcel, Esquisse de la Géographie et de la Végétation des Highlands d'Ecosse. Coloured vegetation map. Paris, 1904.